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ENVIRONMENTAL EFFECTS ON MACRO- AND MICROSTRUCTURAL VARIATION IN SHELL FEATURES OF NATURAL POPULATIONS OF *THAIS LAMELLOSA* (GASTROPODA: THAIDIDAE).

by

Cindy Jean Gratto

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF
Master of Science

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

(SPRING) (1989)

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled ENVIRONMENTAL EFFECTS ON MACRO- AND MICROSTRUCTURAL VARIATION IN SHELL FEATURES OF NATURAL POPULATIONS OF *THAIS LAMELLOSA* (GASTROPODA: THAIDIDAE) submitted by Cindy Jean Gratto in partial fulfilment of the requirements for the degree of Master of Science.

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(Supervisor)

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Date: April 6, 1989

Abstract.

Thais lamellosa hatchlings from five genetically isolated populations were raised in the laboratory under a variety of conditions (different food availabilities, exposure to large crab predators, and varied water temperatures). The collection sites of these five populations differed both in degree of wave exposure and degree of predation pressure. All snails responded similarly to the stimuli presented, regardless of parent population.

Limited food, the presence of crabs, and increased water temperatures induced similar morphological responses in these juveniles: decreased growth in shell length, decreased body growth, and decreased spiral growth. Snails raised at elevated water temperatures and those raised in the presence of crabs produced relatively thick shells. Snails raised in the presence of crabs increased their shell-weight to shell-length and shell-weight to body-weight ratios, while no change was elicited in snails raised with either limited food or elevated water temperatures with respect to these parameters. A number of snails raised in the presence of crabs initiated apertural tooth development; those snails raised in the absence of crabs did not. Shell thickening and apertural tooth secretion in the crab treated snails undoubtably represent predator avoidance responses through shell strengthening. Snails from one site (Argyle Creek) appeared significantly less probable to produce apertural teeth than the remaining four sites. Field-collected adults from this site showed markedly fewer sublethal crab predation scars on their shells than did snails from

Aguilar Point, Cattle Point, and Mar Vista. These data suggest the capacity to respond phenotypically to chemical cues may vary among natural populations. None of the remaining shell and body parameters measured in these experiments, however, exhibited significant differences among sites in response to the presented stimuli.

Shells of *T. lamellosa* are composed of two microstructural layers: an inner aragonitic crossed lamellar layer and an outer calcitic simple irregular prismatic layer. The relative thicknesses of the two shell microstructural layers did not vary in either the food or in the water temperature treatments. Snails raised in the presence of crabs did not vary the thickness of the inner crossed lamellar layer, but the thickness of the outer prismatic layer increased markedly. This increased secretion of prisms may be explained as an attempt to reduce the effect of the inner crossed lamellar layer on the bending strength of the outer surface of the shell. The function of this inner layer may be to increase the resistance of the shell to either crack propagation or to abrasive forces.

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Chapter I.
General Introduction

A conspicuous feature of most gastropods is the secretion of an external shell composed of calcium carbonate. These shells vary substantially among species both in overall form and internal microstructure. Shell forms appear to reflect adaptations to the various life histories of snails. A globose shell, for example, may act as a water reservoir in high intertidal species, where desiccation may be a problem (Lewis, 1963; Vermeij, 1973). External shell sculpture may act to break up the force from waves in areas of high wave exposure (Vermeij, 1978), and in these same areas, an enlarged aperture and foot may reduce the probability of dislodgement (Kitching *et al.*,1966; Kitching & Lockwood, 1974; Heller, 1975; 1976; Etter, 1988). Predation may be hindered by one or a combination of features including a general thickening of the shell, the secretion of external shell structures such as varices, ribs, and spines, and the development of an elongate, dentate aperture (see reviews in Vermeij, 1978; 1987). Although the occurrence of these features is well documented between and within species, little is known of either the genetic or the environmental factors affecting them.

The basic composition of gastropod shells is quite uniform. The shell generally consists of two layers: an outer tough organic periostracum, and an inner primarily calcareous layer, which constitutes the bulk of the shell. This latter layer is composed of calcium carbonate crystals ensheathed in organic material or

matrix. The arrangement of these crystals or prisms describes a particular shell microstructure. See Appendix I for a brief summary of Carter and Clark's (1980) description of some common shell microstructural types. One or more of these microstructures may be found arranged as layers within a single shell. Each of these layers is generally composed of one of two minerals: calcite or aragonite. Both minerals may occur within a single shell (Rhoads & Lutz, 1980). The occurrence of these layers within individuals of a single species has been generally accepted to be uniform, and shell microstructure has been used extensively as a major taxonomic character (Lindberg & Kellogg, 1982; Wellington & Kuris, 1983; Chen, 1985; Lindberg, 1986; Lindberg & Hickman, 1986).

Due to both the crystalline arrangement and the associated organic component, specific mechanical properties are associated with each microstructure. Such properties include bending strength, crushing strength, tensile strength, elasticity, plasticity, resistance to abrasion, and resistance to chemicals such as acids and chelating agents (Currey & Taylor, 1974; Currey, 1976; Gabriel, 1981).

Variations in shell microstructural composition have been strongly associated with life histories (Taylor & Layman, 1972; Gabriel, 1981), and to a lesser degree, environmental conditions (Kennedy *et al.*, 1969; Rhoads & Lutz, 1980). Although shell microstructure is frequently used as a taxonomic character, little work has examined possible phenotypic plasticity within this component of the shell. For this reason I chose to study both shell morphological and microstructural variation in response to

controlled environmental conditions. I also examined the responses of several genetically isolated populations of a single species. Based on these data I assessed i. the genetic and plastic components of both overall shell morphology and shell microstructure, and ii. the inter-relationship between these two components.

Study Animal

The snail *Thais lamellosa* [= *Nucella lamellosa*] (GMELIN, 1791) (Prosobranchia: Thaididae) is found abundantly in the low intertidal zone along the Pacific coast of North America, from the Bering Strait to central California (Morris *et al.*, 1980). *Thais lamellosa* is a predator, feeding primarily on barnacles and mussels by drilling their calcareous shells through the use of both radula and accessory boring organ (Morris *et al.*, 1980).

These snails exhibit direct development. In the field sexual maturity is reached during their fourth year, and snails generally return to their hatching site, where breeding takes place in aggregations. Because snails generally return to the same breeding site over a period of years, breeding aggregations are persistent (Spight, 1974). Also, because of a low adult mobility, populations tend to be genetically isolated, and a large number of these isolates may be found within a relatively small geographic range (Grant & Utter, 1988).

Thais lamellosa is morphologically highly variable. The shell may range from very thin, with marked axial fluting and spiral

ribbing to heavy and thick, with little development of surface sculpture other than non-distinct spiral ribs and a pronounced development of apertural teeth (Kincaid, 1957). The shell morphology within a population is usually quite uniform (Spight, 1973). The morphological variation observed between populations of this species appears to be due, at least in part, to an environmental response to a common predator, the red rock crab, *Cancer productus* RANDALL, 1839 (Appleton & Palmer, 1988).

The shell of *T. lamellosa* is composed of two microstructural layers (see Chapter III), similar to those of *T. lapillus*, consisting of an outer calcitic simple irregular prismatic layer and an inner aragonitic crossed lamellar layer (Bøggild, 1930). These findings are in contradiction with Vermeij and Currey (1980), who found both *T. lamellosa* and *T. lapillus* to be of an "ill-defined cross-lamellar" microstructure. I believe these apparent differences in opinion lie in the method of examination of the microstructures: Vermeij and Currey (1980) determined microstructural types solely with scanning electron microscopy, while Bøggild (1930) used thin sections, and I used both thin sections (Chapter III) and scanning electron microscopy (unpubl.).

Systematic nomenclature

The systematics of the temperate thaidid gastropods has been a source of much confusion. Dexter (1960), for example, cited a letter by Clench who noted that during the years 1942 to 1949 a single thaidid species could be identified by three generic synonyms:

Purpura, *Nucella*, or *Thais*. Even in relatively recent years both *Nucella* (Abbott, 1974; Smith & Carleton, 1975; Morris *et. al.*, 1980) and *Thais* (Morris, 1952, 1973; Kozloff, 1973; Carefoot, 1977; Gosner, 1978) may be found in the general treatese involving gastropods.

The name *Nucella* has primarily been used by the British for no apparent reason other than tradition (Crothers, 1972). In North America, however, this genus has generally been referred to as *Thais* throughout the bulk of the literature, particularly that literature referring to the Pacific coast species (Kincaid, 1957; Spight, 1972, 1973, 1973, 1975a,b, 1976a,b, 1981, 1983; Lyons & Spight, 1973; Spight et. al., 1974; Bertness & Schneider, 1976; Kitching, 1976; Spight & Emlen, 1976; Bertness, 1977; Campbell, 1978; Vermeij & Currey, 1980; Palmer, 1980, 1981, 1985; Appleton & Palmer, 1988). Recent work, however, indicates that these two genera (*Thais* and *Nucella*) are not synonymous and that these temperate thaidids may, in fact, be members of the genus *Nucella* (Kool, 1986; as cited in Kool, 1987). These data, however, have as yet to be published and although the North American temperate species may officially be identified as *Nucella* in the near future, I choose, at this time, to attempt to avoid present confusion by following the North American literature, and continue to refer to these temperate species as members of the genus *Thais* throughout this paper.

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Chapter II.

Shell Morphological Plasticity of *Thais lamellosa* in Response to Environmental Conditions

Introduction

Molluscan shell form may be influenced environmentally by both abiotic and biotic factors. The responses to both of these above factors are genetically controlled to a large extent, but some may be phenotypic (Geisel, 1969; Lewis & Bowman, 1975; Crothers, 1977; Seed, 1980; Emberton, 1982; Kemp & Bertness, 1984).

Temperature, for example, is strongly associated with shell shape and colour (Frank, 1965; Hallam, 1965; Feare; 1970; Philips *et al.*, 1973; Heller & Gadot, 1984; Ramos, 1984; Beukema & Meehan, 1985; Roberts & Kell, 1987). Seasonal effects on shell growth have also been well documented (Frank, 1965, 1969; Blackmore, 1969; Ritz & Crisp, 1970; Sutherland, 1970; Richardson *et al.*, 1980). Changes in salinity (Hallam, 1965; Manzi, 1970; Richardson *et al.*, 1980), high wave action (Menge, 1974; Creese & Underwood, 1976; Menge, 1978; Boyden & Zeldis, 1979; Dudley, 1985; Simpson, 1985), water flow rates (O'Loughlin & Aldrich, 1987; Lam & Calow, 1988), and height in the intertidal zone (Sutherland, 1970; Boyden & Zeldis, 1979) have been found to effect the size and shape of apertural formation, shell shape, and snail growth rate.

Growth rate alone appears to account for a great deal of variation in shell morphology (Rhoads & Lutz, 1980; Vermeij, 1980). High growth rates are associated with the secretion of relatively thin

shells (Gould, 1968; Wellington & Kuris, 1983) with low spires (Gould, 1968; Frank, 1975; Crothers, 1975; Spight, 1973). The secretion of apertural teeth in *Thais lapillus* (Crothers, 1971), and *T. lamellosa* (Appleton & Palmer, 1988), as well as inner ridges in the aperture of *Stagnicola elodes* (Jokinen, 1977) have been attributed to growth stoppages, although Appleton and Palmer (1988) found greater tooth development to be correlated with the presence of predatory crabs.

Growth rate and shell shape may also be affected by habitat quality, which includes amount of food items available (Leighton & Boolootian, 1963; Phillips & Campbell, 1968; Laxton, 1970a; Hughes, 1972; Stimson, 1973; Eversole, 1978). Also associated with feeding, and subsequently habitat quality and growth rate, are intraspecific (Seed, 1968; Sutherland, 1970; Black, 1977; Choat, 1977; Creese & Underwood, 1982; Ortega, 1985; Ahmed *et al.*, 1986) and interspecific (Haven, 1973; Choat, 1977; Choat & Black, 1979; Creese & Underwood, 1982; Schoener, 1983) competition, as well as predation pressures (Paine, 1969; Hamilton, 1976, 1977; Markowitz, 1980; Bertness & Cunningham, 1981; Garrity & Levings, 1981; Garrity, 1984).

A number of shell characteristics appear to have evolved in response to predation pressure. The effectiveness of a particular trait, however, depends upon the mode of predation. Some predators are capable of extracting body parts through the shell aperture of a snail without damaging the shell itself, some predators break the shell to extract the animal, others swallow the prey whole, and still others are capable of drilling through shells (see Vermeij, 1987, for

a review). Proposed predator avoidance responses in shell morphology include an unwieldy size or shape of an individual (Vermeij, 1978), the secretion of a thick shell (Vermeij, 1978; Bertness & Cunningham, 1981; Palmer, 1985), the development of an elongate or reduced aperture, the development of apertural structures such as teeth or a tight-fitting operculum (Vermeij, 1978; Bertness & Cunningham, 1981; Heath, 1985; Signor, 1985; Appleton & Palmer, 1988), and the secretion of strong external shell sculpturing (Spight & Lyon, 1974; Palmer, 1979; Vermeij, 1978; Bertness & Cunningham, 1981).

Thick shells, highly ornamented external surfaces, lower spires, and elongate, occluded apertures are found more commonly in tropical regions as opposed to temperate (Vermeij, 1978). Vermeij (1978) correlates this trend with higher predation pressures in regions of lower latitudes. Similarly, the greater prevalence of these same features in snails from the Pacific and Indian Oceans, relative to those of the Atlantic is also correlated with predation levels (Vermeij, 1973).

That both the biotic and abiotic factors of an environment influence snail growth and shell morphology is obvious. What is not obvious are the costs incurred by these snails as a result of these variations. The cost of the production of a calcium carbonate skeleton, for example, has been attributed to three major factors: i. the energetic expense of the actual secretion of the shell material, ii. the energetic expense of transporting this skeleton, once formed, and iii. a non-energetic cost due to body growth-rate limitations imposed by the maximal rate at which shell material may be

physically deposited (Palmer, 1981). Pre-reproductive rates of body growth and final body size have been found to be directly proportional to reproductive output (Spight, 1981). In many species, body growth does not continue significantly past maturity (Spight, 1981). Rates of shell and subsequent body growth are, therefore, of marked importance to the fitness of an individual. Shell shape and shell structure figure prominently as factors: shell thickness and spire height are inversely proportional to maximal body growth (Spight, 1981).

Snail shell and body growth represent a balance determined, at least to some extent, by the environment. Through the examination of a number of populations of snails, it may be possible to determine what stimuli may affect shell and body growth; what effect these stimuli may have on such growth parameters, and how these responses vary across a number of populations.

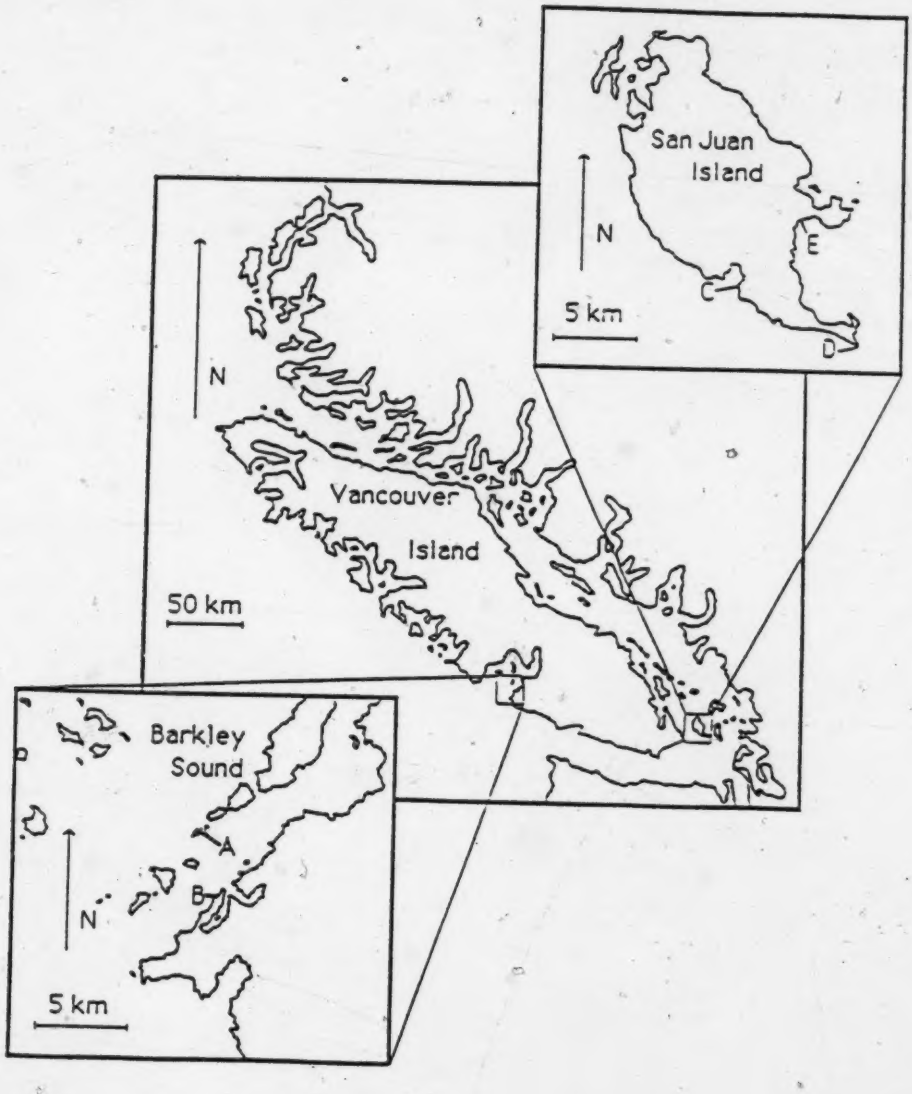
Methods

I. Collection sites and raising of hatchlings.

Adult individuals of *Thais lamellosa* were collected from five study sites (Figure II-1) in the Pacific Northwest in September of 1986. These sites included Aguilar Point (48°50'18"N, 125°18'24"W) and Sanford Island (48°52'18"N, 125°09'48"W), Barkley Sound, British Columbia, and Cattle Point (48°27'06"N, 122°57'42"W), Mar Vista (48°28'48"N, 123°04'W), and Argyle Creek (48°31'06"N, 123°00'48"W), San Juan Island, Washington. All sites varied with respect to degree of wave exposure and large crab predators, such as

Figure II-1.

Map of study sites. A = Sanford Island, B = Aguilar Point, C = Mar Vista, D = Cattle Point, E = Argyle Creek.


San Juan
Island
N
5 km
C
D
E
N
Vancouver
Island
50 km
Barkley
Sound
A
B
N
5 km

Cancer productus (see Table II-1). Both Argyle Creek and Sanford Island are relatively sheltered locations with low crab predation pressures. Mar Vista is semi-exposed with high predation pressures, ans Aguilar Point and Cattle Point are exposed with low predation pressures at Cattle Point, and relatively higher predation pressures at Aguilar Point. See Appendix 2 for an explanation of the collection of the data and the calculation of the wave exposure index.

The snails were maintained in cages submerged in water tables supplied with a flow rate of approximately 50 mL/s at the Bamfield Marine Station, Bamfield, British Columbia, Canada. The cages were constructed by removing two opposing sides of plastic freezer containers (Frig-O-Seal) and replacing them with screening held in place with hot melt glue.

In late December and early January the adults began to lay eggs, which were removed and placed in a direct flow of water in screen pouches (mesh size of approximately 1 mm). After three months the screen pouches were placed into cages with a mesh size of 67 μm and within one month the eggs had completely hatched. Rocks with juvenile barnacles (*Balanus glandula*) were added to the cages as food for the hatchlings. These rocks were collected from a site with no native *T. lamellosa*. The barnacles were replaced as necessary, usually at monthly intervals, although cages were checked biweekly. Barnacle replacement coincided with a monthly cage cleaning.

Table II-1. Relative degrees of wave exposures and predation pressures at all five collection sites. SE = standard error, N = number of samples

Site	Wave exposure index*			Predation pressure index†	
	Mean	SE	N	Percent	N
Argyle Crk.	22.86	1.52	3	5.71	132
Aguilar Pt.	144.78	6.76	3	8.20	117
Cattle Pt.	149.86	6.10	3	1.47	152
Mar Vista	128.27	4.23	3	22.73	143
Sanford Is.	101.60	3.53	3	0.00	140

* Height in centimetres from the top of the barnacle zone to the base of the vascular plants. See Appendix 2 for the derivation of this height.

† Percentage of adult snails bearing sublethal predation scars on their shells. This measurement approximates predation pressures, as it only measures snails not killed by predator attacks, and assumes those killed are proportional to those scarred.

II. Measurements.

At the initiation of the experiments, and at monthly intervals thereafter, three measurements were taken on each tagged individual: shell length (from the apex to the distal-most tip of the siphonal canal), weight of the snail immersed in sea water, and weight of the snail in air. Weight in air was measured after the snails were chased into their shells and any water remaining in the shell aperture was removed by blotting with Kimwipes. These latter two measurements were later used to approximate dry shell weight and dry body weight (Palmer, 1982). See Appendix 3 for a summary of the calculations used to determine these dry weights. At both the initiation and the termination of the experiments, the outer lip of the aperture was marked with enamel paint. These marks were later used to calculate shell spiral growth, as the spiral distance between the old and new apertural lip. This distance was measured by calibrating a length of flexible wire and coiling it around the shell along the posterior-most spiral rib of the shell whorls, between the marks. An approximation to translation rate was calculated by dividing the spiral growth distance by shell length change. In using this method of determining translation rate, the assumption that spiral growth does not occur upwards, towards the spire must be made. Shells of *Thais lamellosa* do not appear to have such a type of growth.

At the end of the three month experimental period, all snails were terminated and their bodies removed from the shells with forceps. The shells were air dried for at least forty-eight hours before being cut for thin sections (see Methods, Chapter III for a

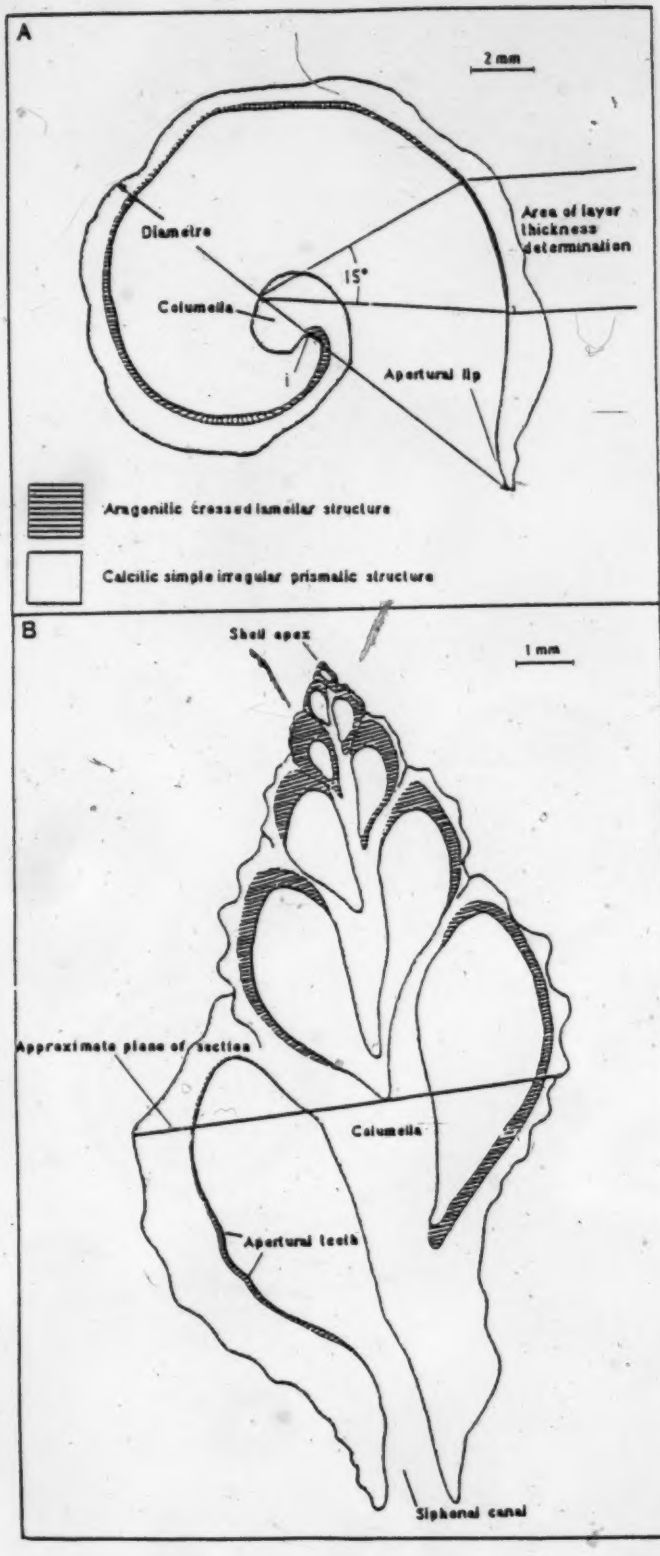
description of the thin sectioning technique). The sections were cut through the posterior-most spiral rib of the body whorl, perpendicular both to the growth lines and to the outer surface of the shell, (see Figure II-2). Thin sections were examined with a dissecting microscope and camera lucida drawings were made from the magnified resulting thin sections. The area of the shell over a set distance was measured from these drawings with a MacIntosh 512 Summographics tablet, using the MacIntosh MacMeasure program. One fixed endpoint of this area calculation was determined as the last point of secretion of crossed lamellar microstructure (see Chapter III) from the shell aperture. The distance of the measurement was determined by approximating the section to be a circle, estimating a diameter (across the body whorl, starting at the apertural lip and passing through point i, the indentation of the shell just prior to the columella), and calculating an arc length for an angle of 15°. This distance was extended from the fixed endpoint towards the columella, or away from the apertural lip (see Figure II-2 for a diagramatic view). Shell thickness was then estimated by dividing the calculated area by the distance over which it was measured.

After the initial cut had been made on the shells, each shell was examined for apertural tooth development. Apertural tooth development was scored as follows. A value of one was given to a snail exhibiting no sign of apertural tooth development. The value two was assigned if apertural tooth development consisted solely of two or more slight swellings, no more than 0.5 mm in height. Three designated snails with moderately defined apertural teeth, with a

Figure II-2.

A. Diagrammatic view of a representative cross-sectional cut through the shell of a juvenile laboratory-raised *Thais lamellosa*. The section was cut along the posterior-most spiral rib of the body whorl, approximately perpendicular to both the external surface of the shell and to the surface growth lines of the shell.

B. Diagrammatic view of a representative longitudinal section through the shell of a juvenile laboratory-raised *Thais lamellosa*. The section was cut through the longitudinal axis of the shell, from the apex to the siphonal canal. Note the plane of section identifying the region of a cross-sectional cut, such as is represented above, in A.


A
2 mm
Diametre
Area of layer thickness determination
15°
Columella
Aperturul lip
Aragonitic crossed lamellar structure
Calcitic simple irregular prismatic structure
B
Shell apex
1 mm
Approximate plane of section
Columella
Aperturul teeth
Siphonal canal

height greater than 0.5 mm, but with an angle of tooth development from the tooth base to be less than 30°. The value four was assigned if tooth development was well-defined in both tooth height and in their angle of development (ie. steep-sided, with an angle greater than 30°, as measured from the tooth base).

III. Experimental design.

At a post-hatching age of approximately four months, the last week of August, 1987, snails of approximately equal size were randomly separated into treatment groups, with ten to fifteen animals per group. Each group was then transferred to a single cage with a mesh size of approximately one mm. At all times snails from different sites were maintained in separate cages. All snails of sufficient size at the initiation of the experiments, were numbered with Brady wire labels and coated with a drop of Krazy glue. All experiments were conducted over a period of approximately three months, from the first of September to the end of November, 1988.

A. Food availability.

Three sets of treatments were established for each of the five study sites: 33%, 67%, and 100% food availability. Snails in the 100% food availability category were maintained with a constant supply of barnacles. The barnacles in the cages of snails maintained with food availabilities of 33% and 67% food, were removed from the cages for six and three days of each nine, respectively. Past work (Appleton & Palmer, 1988) has indicated a removal procedure such as described above, does limit the food intake of *Thais lamellosa*. In all treatments, the barnacles were replaced with

Figure II-3.

Diagrammatic representation of the top view of the experimental designs used in this paper. The large case letters A, B, and C represent the food availability, crab exposure, and water temperature experiments, respectively. Replicates for experimental designs A and B were identical to the representations here, but were conducted in separate water tables. The small case letters a to f represent food and temperature treatments: a = snails fed 33%, b = snails fed 67%, c = snails fed 100%, d = snails raised at ambient water temperature (9-11°C), e = snails raised at a water temperature of 15°C, and f = snails raised at a water temperature of 18°C. The labels d', e', and f' represent the replicate treatments of snail cages d, e, and f.

= water table of constantly flowing sea water

= aquarium of recirculating sea water

= aquarium of constantly flowing sea water

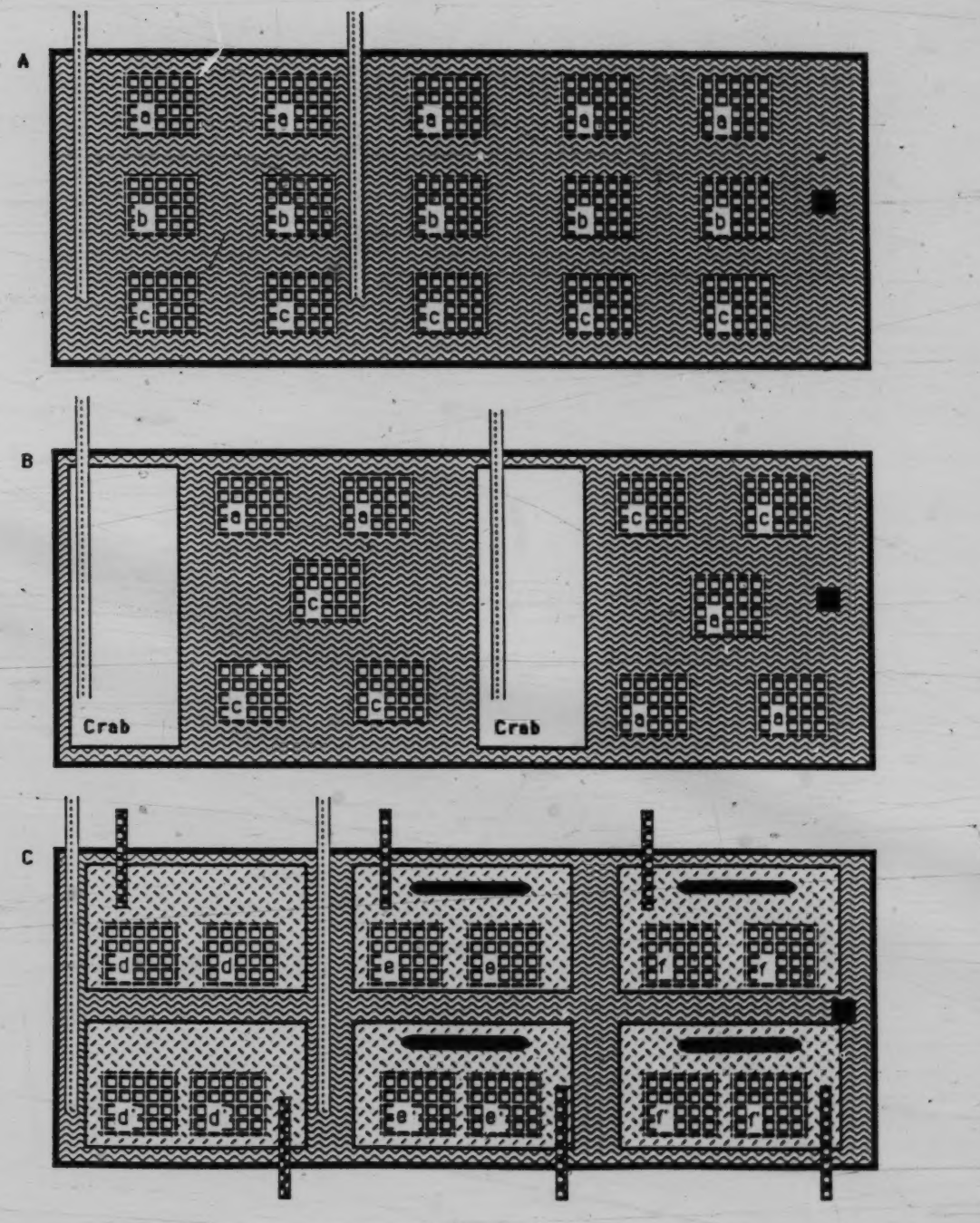
= snail cage

= sea water outflow

= sea water inflow

= air inflow

= submersible water heater


A
Fa
Fb
Fc
B
Crab
Crab
C
Fd
Fe
Ff

fresh field collected individuals monthly. Only a small proportion, approximately 15%, of the barnacles available to the snails had been consumed by the end of each month. All treatments were maintained in individual cages, and two sets of replicates were established. The two sets of replicates were maintained constantly immersed in separate water tables (see Figure II-3A for a diagrammatic view of the experimental set-up). The placement of the individual cages within each water table was changed bimonthly.

B. Predation pressures.

Two treatment groups were established for each of the five study sites. These two treatments consisted of 33% and 100% food availabilities (see Experiment A for a description of the feeding regimes). In both of these treatments, the snails were maintained in separate cages, with two sets of replicates in separate water tables. Two aquaria, each containing a red rock crab, *C. productus*, were added to each of two water tables. Water was maintained at an approximately 50mL/s rate of flow, and all water flowing into each of these water tables first ran through the respective aquaria containing the crabs. The snails in these treatments, therefore, could detect the presence of, but had no actual contact with the crabs (Figure II-3B). The four crabs were fed field-collected individuals of *T. lamellosa*, and the number of snails consumed by each of the crabs was recorded. Again, barnacles were replaced monthly (less than 15% were consumed each month) and the placement of individual cages within the water table was changed bimonthly. The controls for these two treatments were the 33% and

100% food availability treatments of Experiment A, maintained in the absence of crab effluent.

C. Temperature.

Three treatments were established for each of two study sites (Argyle Creek and Mar Vista). All treatments were carried out in five gallon aquaria with recirculating water, maintained in a full water table of constantly flowing sea water at an approximately 50mL/s flow rate (Figure II-3C). The water in each of these aquaria was replaced with clean water of the same temperature every two weeks. One aquarium was kept at ambient sea water temperature (approximately 9° to 11°C), while the other two aquaria were equipped with Hägen 150 W submersible heaters. One of these latter two aquaria was maintained at 15°C and the other at 18°C and barnacles were replaced monthly. Food was not limited. Two replicates were conducted in separate recirculating aquaria within the same water table.

IV. Statistical analyses.

Pre-experimental differences among treatments in shell length, dry shell weight, and dry body weight were tested with two-way ANOVAs (site and treatment). ANOVAs were conducted on each replicate separately because the purpose of these tests was to compare pre-experimental values across site and treatment, only.

The degree of variation between replicates with respect to final shell and body parameters (shell length, dry shell weight, dry body

weight) was tested through one of two methods, depending on the type of experimental design. The experimental design of the food availability experiment consisted of two fixed (site and food) and one random (replicate) variables. Because all cages for one replicate were in a single water table, and all cages for the second replicate were located in a separate water table, the replicate factor is fully crossed with both the site and food factors, and may be considered as a 'water table' affect. A three-way factoria! analysis of variance (ANOVA) was conducted on the food experiment data, and the F-values for site, food and the site-food interaction term were calculated as suggested by Sokol and Rohlf, 1981 (pp. 382-383) for a mixed model ANOVA (A,B fixed, C random). The mean square (MS) for sites (A) was divided by the site-replicate interaction (AC) MS to calculate the F-value for sites. Similarly the food (B) and the site-food interaction (AB) were divided by the food-replicate and the site-food-replicate interaction terms, respectively. The F- values for the remaining mean squares of replicate (C), site-replicate (AC), food-replicate (BC), and the site-food-replicate (ABC) were calculated by dividing by the error MS. Exact P-values were calculated with a Hewlett-Packard 67 programmable calculator.

The experimental design of the crab-exposure and the water temperature experiments were different from the food availability experiment, and the analyses were conducted differently. For both experiments, replicates for one treatment were held in different aquaria than those for the second treatment (Figure II-3). Consequently, replicates were most appropriately considered nested

within main effects. To circumvent the limited ability of most statistical routines to compute the proper F-values for such a design, the relative effects of replicate versus site and treatment (crab-exposure or water temperature) on snail growth were examined with three-way factorial (ANOVA), and subsequent calculation of F-values as suggested by Hartley (1962) and Sokol and Rohlf (1981). This method designates replicates as a "dummy" variable and may be explained as follows. The sums of squares for sites (A), treatment (B), and replicates (C) were computed through the three-way ANOVA as if each were crossed in a fully factorial design. The sums of squares for the replicate variable (C) and the interaction terms in which it was included (AC, BC, ABC) were summed. The mean squares (MS) for replicates was recalculated by dividing the resultant total replicate sums of squares by the summed degrees of freedom for these same four terms (C, AC, BC, ABC). F-values were then calculated by individually dividing the MS for sites (A), food availability (B), and their interaction term (AB) by the recalculated MS value. The F-value for replicates was then calculated by dividing the new replicate MS value by the error MS. Exact P-values were calculated using a Hewlett-Packard 67 programmable calculator.

Variation in final shell and body parameters (shell length, dry shell weight, dry body weight), spiral growth, and relative translation rate (spiral growth/shell length change), were examined through regression and analyses of covariance (ANCOVA) (final plotted against initial growth values) where possible, and through ANOVAs otherwise. In cases where the linearity of the plots was

questionable or when a relatively large number of regressions were of unequal slopes (shell length, shell weight, and body weight), both of these analyses were conducted.

Due to a number of unusable thin sections, a number of cells for shell thickness measurements were either empty or unequal. In order to provide equal cells for the ANOVAs, a number of data points were randomly excluded from the analyses. Because of empty cells, only snails from Mar Vista and Sanford Island were included in the shell thickness analyses. Otherwise, the ANOVA was conducted as described previously.

Because of empty cells, all sites were pooled for snails fed 33% in the crab-exposure experiment. A nested two-way ANOVA (crab-exposure and replicates) was conducted on these data because both the crab-presence and crab-absence treatments, as well as the replicates for the crab-exposure factors were located in separate water tables (see Figure II-3).

Due to an empty cell in the data of snails from the water temperature experiment, initial analyses were conducted on snails from Argyle Creek only. Because both the water temperature treatments and each of their replicates were conducted in separate aquaria, a two-way nested ANOVA (temperature and replicates) was conducted on these data. In order to test for site differences, a two-way factorial ANOVA (site and temperature) was conducted on snails from both Argyle Creek and Mar Vista, but for replicate one, only. The resultant design was factorial in nature, but was limited in its ability to test for temperature differences due to possible aquarium effects, which could not be factored out.

Differences in final and initial relative weight of dry shell versus shell length and dry body weight respectively were examined through ANCOVAs, although these analyses revealed some regressions to be of unequal slopes. The scattergrams of these data (Figures II- 5-8, 11-14, 17-18) indicate slope differences to be probably due to the small amount of scatter about each regression. Because of the similarity in slopes, indicated by these scattergrams, ANCOVAs were conducted on these data. Initial measurements of shell and body parameters were conducted over a period of three days, during which, the experiments were in progress. In an attempt to factor out any initial effects of the experimental stimuli, initial shell weight was added as a second covariate for the final shell weight comparisons.

Contingency table analyses were conducted for site, food availability, and replicates versus the presence versus absence of apertural tooth development.

All ANOVAs, contingency tables, and basic statistics were conducted using Statview 512+TM microcomputor package (Abacas Concepts, Berkley, Ca.) and all ANCOVAs with a main frame MIDAS (Statistical Research Laboratory, University of Michigan) statistical package.

Results

Initial shell morphology.

Comparisons of pre-experimental shell and body parameters (shell length, dry shell weight, dry body weight) revealed no

Table II - 2: Means and standard errors of initial and final shell and body parametres of *Thais lamellosa* juveniles raised at varying crab exposures and food availabilities. SE = standard error, N = sample size

Food	Treatment	Study site	Replicate	Shell length (cm)				Dry shell weight (g)				Dry body weight (g)				Spiral growth (cm)		N	Final shell thickness(mm)			Percent mortality
				Initial		Final		Initial		Final		Initial		Final								
				Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		Mean	SE	N	
Fed 33 %	No crabs	Argyle Crk.	1	1.107	0.114	2.353	0.197	0.112	0.031	0.573	0.131	0.016	0.005	0.158	0.041	1.744	0.263	10	-	-	-	0
		Aguilar Pt.	1	1.192	0.073	1.946	0.139	0.108	0.017	0.553	0.087	0.017	0.003	0.079	0.016	1.950	0.136	8	-	-	-	7
		Cattle Pt.	1	1.215	0.073	2.146	0.132	0.106	0.014	0.646	0.086	0.020	0.003	0.112	0.016	2.143	0.248	13	-	-	-	0
		Mar Vista	1	1.097	0.112	1.963	0.132	0.103	0.029	0.497	0.094	0.019	0.006	0.085	0.017	1.846	0.146	13	0.731	0.079	7	0
		Sanford Is.	1	1.262	0.101	2.028	0.121	0.134	0.026	0.502	0.061	0.024	0.005	0.076	0.013	2.164	0.280	11	0.860	0.133	5	0
		Argyle Crk.	2	1.258	0.130	2.144	0.182	0.126	0.030	0.582	0.118	0.022	0.006	0.092	0.019	2.121	0.182	6	0.876	0.067	5	11
		Aguilar Pt.	2	1.113	0.072	1.857	0.154	0.094	0.017	0.416	0.069	0.014	0.003	0.054	0.011	1.562	0.156	10	1.307	0.305	3	8
		Cattle Pt.	2	1.152	0.059	2.087	0.103	0.096	0.015	0.609	0.077	0.014	0.003	0.089	0.015	2.214	0.300	13	0.869	0.053	8	0
		Mar Vista	2	1.248	0.121	2.102	0.146	0.131	0.035	0.595	0.110	0.025	0.007	0.097	0.021	1.754	0.178	12	0.853	0.049	3	0
		Sanford Is.	2	1.165	0.106	2.051	0.140	0.106	0.026	0.554	0.093	0.018	0.005	0.076	0.018	2.300	0.302	10	0.668	0.090	3	9
Fed 33 %	Crabs	Argyle Crk.	1	1.190	0.069	2.164	0.133	0.133	0.023	0.869	0.152	0.012	0.002	0.123	0.023	2.242	0.203	12	-	-	-	0
		Aguilar Pt.	1	0.992	0.063	1.814	0.138	0.082	0.016	0.657	0.133	0.009	0.001	0.061	0.013	1.906	0.254	7	-	-	-	12
		Cattle Pt.	1	1.029	0.076	1.992	0.145	0.087	0.018	0.721	0.172	0.011	0.002	0.089	0.018	1.782	0.173	11	1.026	-	1	15
		Mar Vista	1	1.057	0.116	1.842	0.184	0.119	0.034	0.698	0.206	0.012	0.003	0.083	0.023	1.408	0.255	11	1.314	0.439	2	8
		Sanford Is.	1	1.103	0.085	1.625	0.108	0.108	0.024	0.481	0.129	0.015	0.003	0.082	0.020	1.489	0.273	10	1.357	0.252	3	0
		Argyle Crk.	2	1.264	0.097	1.859	0.130	0.160	0.035	0.616	0.149	0.016	0.004	0.068	0.017	1.291	0.101	9	1.507	0.206	5	0
		Aguilar Pt.	2	1.180	0.117	1.792	0.190	0.147	0.040	0.673	0.221	0.040	0.017	0.055	0.020	0.886	0.146	9	-	-	-	0
		Cattle Pt.	2	1.152	0.059	2.087	0.103	0.096	0.015	0.786	0.136	0.017	0.003	0.070	0.011	1.400	0.323	13	1.568	0.060	8	7
		Mar Vista	2	1.207	0.115	2.134	0.154	0.153	0.044	1.008	0.200	0.020	0.005	0.090	0.022	1.450	0.167	12	-	-	-	7
		Sanford Is.	2	1.132	0.100	1.800	0.180	0.126	0.029	0.625	0.149	0.013	0.003	0.053	0.013	0.850	0.167	10	2.303	0.038	2	9
Fed 67 %	No crabs	Argyle Crk.	1	1.195	0.088	2.626	0.089	0.130	0.025	1.026	0.101	0.016	0.004	0.207	0.022	3.786	0.404	11	0.462	0.035	8	0
		Aguilar Pt.	1	1.155	0.081	2.370	0.125	0.108	0.019	0.830	0.097	0.018	0.003	0.132	0.019	3.614	0.216	11	0.667	0.181	3	0
		Cattle Pt.	1	1.132	0.089	2.625	0.122	0.099	0.023	1.048	0.134	0.019	0.004	0.186	0.025	4.113	0.333	12	0.504	0.039	8	7
		Mar Vista	1	1.183	0.129	2.655	0.144	0.146	0.050	1.070	0.166	0.028	0.010	0.195	0.033	3.593	0.385	14	0.543	0.058	10	7
		Sanford Is.	1	1.168	0.085	2.354	0.140	0.113	0.021	0.745	0.117	0.019	0.004	0.125	0.022	2.922	0.225	9	0.525	0.181	3	9
		Argyle Crk.	2	1.317	0.048	2.266	0.130	0.129	0.013	0.698	0.086	0.020	0.002	0.113	0.015	2.729	0.221	10	0.583	0.056	7	8
		Aguilar Pt.	2	1.270	0.071	2.355	0.135	0.140	0.022	0.883	0.126	0.021	0.004	0.135	0.022	3.217	0.466	12	0.651	0.063	7	8
		Cattle Pt.	2	1.166	0.065	2.336	0.099	0.102	0.015	0.774	0.089	0.018	0.003	0.136	0.017	3.338	0.370	13	0.632	0.053	6	0
		Mar Vista	2	1.227	0.150	2.259	0.172	0.137	0.054	0.726	0.124	0.026	0.012	0.143	0.041	3.406	0.299	10	0.446	0.057	5	0

Table II-2. continued.

Food	Treatment	Study site	Replicate	Shell length (cm)				Dry shell weight (g)				Dry body weight (g)				Spiral growth (cm)		N	Final shell thickness(mm)			Percent mortality
				Initial		Final		Initial		Final		Initial		Final								
				Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		Mean	SE	N	
Fed 100 %	No crabs	Argyle Crk.	1	1.196	0.104	2.475	0.15	0.125	0.026	0.850	0.127	0.018	0.004	0.147	0.024	3.214	0.324	11	0.700	0.080	11	0
		Aguilar Pt.	1	1.231	0.084	2.672	0.089	0.128	0.020	1.157	0.085	0.022	0.004	0.186	0.016	3.219	0.181	9	0.826	0.061	5	10
		Cattle Pt.	1	1.073	0.062	2.454	0.098	0.083	0.013	0.849	0.093	0.015	0.002	0.170	0.020	3.939	0.304	15	0.687	0.066	15	0
		Mar Vista	1	0.990	0.093	2.216	0.079	0.073	0.022	0.593	0.062	0.022	0.014	0.120	0.014	3.177	0.174	13	0.575	0.108	13	7
		Sanford Is.	1	1.166	0.098	2.385	0.149	0.116	0.025	0.794	0.120	0.019	0.004	0.140	0.024	3.417	0.239	9	0.566	0.119	9	0
		Argyle Crk.	2	1.336	0.070	2.475	0.137	0.137	0.018	0.877	0.132	0.023	0.003	0.160	0.027	3.352	0.365	10	0.563	0.068	5	7
		Aguilar Pt.	2	1.331	0.074	2.298	0.128	0.150	0.025	0.764	0.098	0.021	0.005	0.150	0.026	2.945	0.299	10	0.714	0.063	6	7
		Cattle Pt.	2	1.184	0.096	2.374	0.106	0.104	0.022	0.765	0.095	0.018	0.004	0.123	0.017	3.000	0.285	11	0.501	0.081	7	0
		Mar Vista	2	1.298	0.103	2.511	0.138	0.141	0.030	0.924	0.137	0.026	0.006	0.162	0.025	2.987	0.190	12	0.718	0.109	7	8
		Sanford Is.	2	1.175	0.089	2.672	0.107	0.107	0.022	1.043	0.101	0.020	0.004	0.171	0.020	4.695	0.390	11	0.673	0.044	4	0
Fed 100 %	Crabs	Argyle Crk.	1	0.999	0.128	2.132	0.199	0.102	0.036	0.819	0.228	0.007	0.002	0.124	0.038	2.713	0.302	7	1.120	0.199	4	0
		Aguilar Pt.	1	1.161	0.076	2.365	0.160	0.135	0.024	1.272	0.197	0.013	0.002	0.146	0.025	3.220	0.215	10	1.216	0.124	6	0
		Cattle Pt.	1	0.957	0.056	2.229	0.092	0.067	0.012	0.957	0.118	0.009	0.001	0.117	0.013	3.050	0.201	13	0.853	0.080	9	0
		Mar Vista	1	1.029	0.086	2.254	0.128	0.100	0.026	1.084	0.203	0.013	0.003	0.143	0.007	3.125	0.125	14	0.870	0.074	6	14
		Sanford Is.	1	1.084	0.097	2.186	0.175	0.111	0.023	0.886	0.176	0.013	0.002	0.118	0.022	2.920	0.231	10	0.999	0.099	4	0
		Argyle Crk.	2	1.098	0.067	1.841	0.080	0.098	0.018	0.548	0.074	0.013	0.002	0.050	0.006	1.527	0.124	10	1.342	0.215	7	0
		Aguilar Pt.	2	1.141	0.068	1.939	0.088	0.120	0.022	0.742	0.107	0.013	0.002	0.060	0.010	1.771	0.124	11	1.575	0.145	9	7
		Cattle Pt.	2	1.168	0.064	2.113	0.091	0.118	0.020	0.827	0.092	0.014	0.002	0.077	0.010	1.664	0.141	13	1.357	0.225	4	0
		Mar Vista	2	1.086	0.086	2.055	0.128	0.105	0.025	0.835	0.165	0.012	0.003	0.077	0.016	1.991	0.166	13	1.412	0.245	8	7
		Sanford Is.	2	1.178	0.104	1.934	0.137	0.132	0.032	0.720	0.157	0.014	0.003	0.067	0.017	1.706	0.163	9	1.393	0.262	9	0

Table II - 3: Means and standard errors of initial and final shell and body parametres of *Thais lamellosa* juveniles raised at varying sea water temperatures. SE = standard error, N = sample size

Temperature	Study site	Replicate	Shell length (cm)				Dry shell weight (g)				Dry body weight (g)				Spiral growth (cm)		N	Final shell thickness(mm)			Percent mortality
			Initial		Final		Initial		Final		Initial		Final								
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		Mean	SE	N	
Ambient (9-11°C)	Argyle Crk.	1	0.927	0.037	2.031	0.071	0.050	0.006	0.375	0.036	0.008	0.001	0.081	0.008	3.018	0.268	11	0.295	0.105	3	15
	Mar Vista	1	1.121	0.074	2.283	0.111	0.082	0.014	0.489	0.059	0.015	0.003	0.123	0.018	3.138	0.392	11	0.410	0.051	5	0
	Argyle Crk.	2	1.075	0.055	2.423	0.076	0.073	0.010	0.496	0.047	0.014	0.002	0.120	0.009	4.229	0.286	15	0.259	0.016	6	12
	Mar Vista	2	1.119	0.087	2.374	0.184	0.082	0.017	0.481	0.076	0.016	0.003	0.120	0.023	3.557	0.295	7	-	-	-	22
15 °C	Argyle Crk.	1	1.140	0.052	1.907	0.071	0.083	0.010	0.387	0.042	0.018	0.002	0.077	0.011	0.562	0.057	11	0.390	0.019	5	21
	Mar Vista	1	1.208	0.097	1.666	0.069	0.105	0.032	0.277	0.026	0.023	0.008	0.042	0.006	0.773	0.073	9	0.596	0.062	7	40
	Argyle Crk.	2	1.060	0.052	1.880	0.084	0.075	0.010	0.341	0.033	0.013	0.001	0.065	0.011	1.821	0.444	7	0.592	0.067	3	59
	Mar Vista	2	1.000	0.052	1.895	0.240	0.095	0.028	0.398	0.102	0.017	0.005	0.077	0.023	1.512	0.120	4	0.273	-	1	71
18 °C	Argyle Crk.	1	1.063	0.041	0.677	0.076	0.072	0.007	0.317	0.034	0.013	0.002	0.057	0.007	1.233	0.209	15	0.540	0.120	4	0
	Mar Vista	1	1.219	0.110	1.648	0.113	0.111	0.030	0.357	0.070	0.023	0.007	0.055	0.013	0.511	0.091	9	0.516	0.065	6	36
	Argyle Crk.	2	1.209	0.047	1.755	0.079	0.109	0.011	0.404	0.040	0.019	0.003	0.062	0.007	1.000	0.259	14	0.534	0.051	8	13
	Mar Vista	2	1.303	0.110	1.743	0.095	0.139	0.032	0.400	0.064	0.029	0.008	0.062	0.011	0.963	0.168	9	0.514	0.061	3	25

significant differences between treatments of the food availability experiment (Means table II-2; ANOVA Table II-4). Snails of the crab presence and water temperature experiments, however, were found to have been unequally grouped initially. Within the crab experiments (Means Table II-2, ANOVA Table II-5) initial shell lengths and shell weights exhibited only marginally significant differences in two instances. The patterns in final growth, however, appeared to be fairly constant among sites, regardless of degree of difference in pre-experimental values (Figures A4-15 to 20). Initial body weight differed in a number of instances, however, but the effect of these differences in initial values appeared to be so slight with respect to the overall responses elicited in these snails that they were regarded as being negligible.

A proportionally larger amount of pre-experimental variation was found within the temperature experimental groups (Means Table II-3, ANOVA Table II-6). These variations, however, were not consistent with final growth values: in fact, in most cases a reversal in trend from pre-experimental to final variation was noted. The observed patterns in final shell morphology appear to be not due to these initial variations, but to persist in spite of them. Again, these initial variations were regarded as negligible.

Final shell morphology.

Food availability.

Both the ANCOVA (Table II-7; means Table II-2) and ANOVA (Table II-8; means Table II-2) analyses revealed significant

Table II - 4. Two-way ANOVA tests for differences among food availability treatments in pre-experimental shell and body parameters of *Thais lamellosa* juveniles raised in the absence of crabs, at ambient water temperature (9-11°C). The data are summarized in Table II-2. df = degrees of freedom, MS = mean square, $P \leq 0.05$ indicates a significant difference between pre-experimental shell or body parameters at a 95% confidence level.

Replicate	Factor	df	Initial shell length		Initial shell weight		Initial body weight	
			MS	P	MS	P	MS	P
1	Site	4	0.018	0.317	0.226	0.123	0.141	0.329
	Food availability	2	0.004	0.778	0.021	0.845	0.011	0.910
	Interaction	8	0.008	0.839	0.067	0.823	0.056	0.880
	Error	157	0.015		0.123		0.121	
2	Site	4	0.011	0.391	0.079	0.452	0.040	0.777
	Food availability	2	0.009	0.431	0.131	0.220	0.079	0.418
	Interaction	8	0.003	0.962	0.034	0.921	0.035	0.925
	Error	147	0.011		0.085		0.090	

Table II - 5. Two-way ANOVA tests for differences between crab exposure treatments in pre-experimental shell and body parameters of *Thais lamellosa* juveniles raised at two food availabilities, at ambient water temperature (9-11°C). The data are summarized in Table II-2. df = degrees of freedom, MS = mean square, P≤ 0.05 indicates a significant difference in shell or body parameters at a 95% confidence level.

Food avail.	Replicate	Factor	df	Initial shell length		Initial shell weight		Initial body weight	
				MS	P	MS	P	MS	P
Fed 33 %	1	Site	4	0.008	0.673	0.084	0.576	0.108	0.368
		Crab	1	0.035	0.118	0.024	0.654	0.788	0.006
		Interaction	4	0.015	0.371	0.112	0.433	0.060	0.660
		Error	100	0.014		0.116		0.100	
	2	Site	4	0.005	0.801	0.025	0.929	0.052	0.719
		Crab	1	0.000	0.874	0.139	0.274	0.098	0.325
		Interaction	4	0.001	0.984	0.030	0.900	0.028	0.889
		Error	96	0.013		0.114		0.100	
Fed 100 %	1	Site	4	0.025	0.140	0.334	0.029	0.151	0.198
		Crab	1	0.032	0.134	0.025	0.645	0.992	0.002
		Interaction	4	0.007	0.714	0.070	0.668	0.123	0.300
		Error	103	0.014		0.118		0.099	
	2	Site	4	0.003	0.914	0.041	0.766	0.015	0.939
		Crab	1	0.056	0.022	0.089	0.322	1.040	0.000
		Interaction	4	0.010	0.434	0.086	0.436	0.051	0.630
		Error	101	0.010		0.090		0.078	

Table II - 6. Two-way ANOVA tests for differences among water temperature treatments in pre-experimental shell and body parameters of *Thais lamellosa* juveniles raised in the absence of crabs, at a full food availability. The data are summarized in Table II-3. df = degrees of freedom, MS = mean square, P≤ 0.05 indicates a significant difference among shell or body parameters at a 95% condidence level.

Replicate	Factor	df	Initial shell length		Initial shell weight		Initial body weight	
			MS	P	MS	P	MS	P
1	Site	1	0.039	0.019	0.163	0.079	0.284	0.037
	Temperature	2	0.021	0.051	0.122	0.101	0.231	0.030
	Interaction	2	0.005	0.502	0.034	0.519	0.036	0.567
	Error	62	0.007		0.051		0.062	
2	Site	1	0.000	0.881	0.031	0.449	0.094	0.219
	Temperature	2	0.026	0.032	0.220	0.022	0.192	0.051
	Interaction	2	0.002	0.781	0.000	0.994	0.004	0.941
	Error	50	0.007		0.053		0.061	

Table II - 7. Tests for differences among food availability treatments using adjusted means of ANCOVA analyses of the logged values of final versus initial shell and body parameters of *Thais lamellosa* juveniles raised in the absence of crabs at ambient water temperature (9-11°C). the data are summarized in Table II-2, Figures II-3; A4-1,2,3. Y = adjusted mean, SE = standard error, P≤ 0.05 indicates a significant difference at a confidence level of 95% in slopes or adjusted means.

Measurement	Site	Food Availability						Common slope		Slope equality	Adjusted means
		Fed 33%		Fed 67%		Fed 100%					
		Y	SE	Y	SE	Y	SE	Slope	SE	(P)	(P)
Log shell length (cm)	Argyle Crk.	0.368	0.013	0.398	0.011	0.424	0.011	0.511	0.068	0.3900	0.0084
	Aguilar Pt.	0.316	0.015	0.380	0.013	0.388	0.015	0.678	0.098	0.1790	0.0020
	Cattle Pt.	0.319	0.010	0.387	0.010	0.392	0.010	0.592	0.062	0.1330	0.0000
	Mar Vista	0.310	0.009	0.408	0.009	0.387	0.009	0.563	0.038	0.0130	0.0000
	Sanford Is.	0.313	0.010	0.366	0.010	0.427	0.010	0.510	0.056	0.5840	0.0000
Log shell weight (g)	Argyle Crk.	-0.113	0.013	-0.035	0.011	-0.009	0.012	0.281	0.025	0.0200	0.0000
	Aguilar Pt.	-0.107	0.015	-0.034	0.013	-0.026	0.014	0.268	0.033	0.3660	0.0004
	Cattle Pt.	-0.111	0.011	-0.038	0.011	-0.040	0.011	0.262	0.026	0.0780	0.0000
	Mar Vista	-0.136	0.010	-0.027	0.010	-0.051	0.010	0.247	0.015	0.0040	0.0000
	Sanford Is.	-0.131	0.011	-0.074	0.012	-0.002	0.011	0.221	0.023	0.4700	0.0000
Log body weight (g)	Argyle Crk.	-0.969	0.052	-0.799	0.045	-0.798	0.047	0.564	0.090	0.1210	0.0290
	Aguilar Pt.	-1.127	0.045	-0.908	0.037	-0.815	0.040	0.711	0.094	0.1690	0.0000
	Cattle Pt.	-1.074	0.034	-0.842	0.034	-0.838	0.033	0.631	0.074	0.1550	0.0000
	Mar Vista	-1.117	0.030	-0.795	0.031	-0.858	0.030	0.618	0.045	0.0430	0.0000
	Sanford Is.	-1.177	0.040	-0.964	0.041	-0.788	0.040	0.511	0.079	0.7850	0.0000

Table II - 8. ANOVA results of tests for differences among food availability treatments of the ratio of final/initial shell and body growth parameters of *Thais lamellosa* juveniles raised in the absence of crabs, at ambient water temperature (9-11°C). The data are summarized in Table II-2, Figures II-3; A4-1,2,3. df = degrees of freedom, MS = mean square, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-value for the site term was calculated by dividing its MS by the MS of the site-replicate term. Similarly, the food MS and the site-food interction MS were divided by the MS for the food-replicate interaction and the site-food-replicate interaction MS, respectively. The remaining MS terms were divided by the error MS to calculate their F-values.

Factors	df	Final shell length/ initial shell length		Final shell weight/ initial shell weight		Final body weight/ inital body weight	
		MS	P	MS	P	MS	P
Site (A)	4	0.011	0.12	0.119	0.31	0.139	0.21
Food avail. (B)	2	0.170	0.04	1.187	0.03	2.107	0.01
Interaction(AB)	8	0.007	0.05	0.042	0.17	0.046	0.45
Replicate (C)	1	0.007	0.21	0.082	0.07	0.070	0.15
AC	4	0.003	0.62	0.069	0.06	0.058	0.18
BC	2	0.008	0.16	0.040	0.26	0.016	0.66
ABC	8	0.002	0.87	0.021	0.68	0.042	0.34
Error	286	0.004		0.030		0.037	

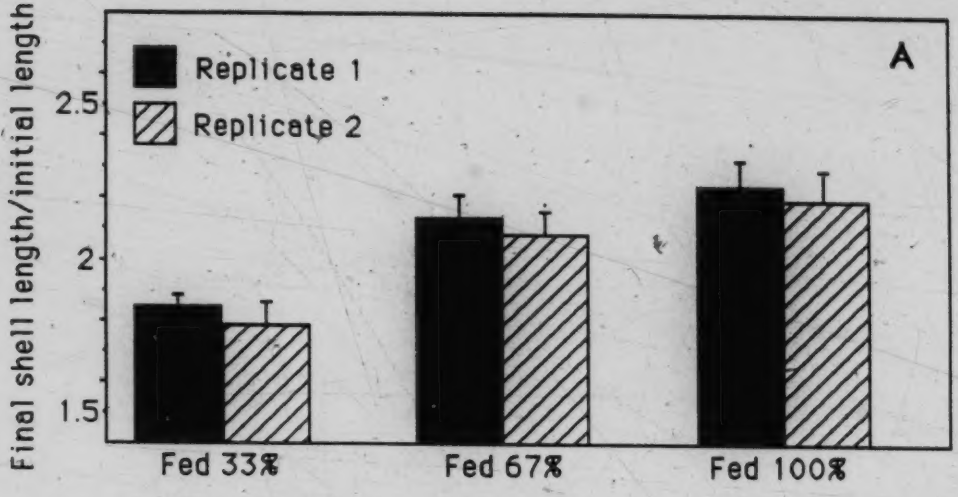
differences in final shell length, shell weight, and body weight among snails exposed to different food availabilities (Figures II-4; A4-1,2,3). Snails raised with a 33% food availability grew less than those of either 67 or 100%. There was little difference in growth between snails from the 67 and 100% food availability treatments. There were no significant site differences with the exception of the site-food interaction term with respect to shell length. The scattergrams of these data (Figure A4-15) do not indicate any apparent site differences.

Analyses of variance results for snails of the 33% food availability treatment, indicate a decrease in rate of spiral growth, an increase in translation rate, and an increase in final shell thickness over snails of the 67% food category (ANOVA Table II-9; means Table II-2; Figures II-5; A4-4,5,6). Translation rate also appeared to be significant between sites at a 90% confidence level, but the scattergram (Figure A4-17) of these data indicates that these differences are slight. The apparent change in translation rate among food availabilities, however, is probably an artifact due simply to differences in spiral growth. When translation rate is plotted against spiral shell growth, no differences between treatments with respect to translation rate are evident (Figure A4-6). Snails raised with 100% food also deposited relatively thick shells (means Table II-2). No significant difference was found between snails of the 67 and 100% food treatments, with the exception of shell thickness.

No significant differences were found between pre-experimental regressions of shell weight on shell length and on body weight,

Figure II-4.

Relative growth in shell length (A) and shell weight (B) of snails from the food availability experiment. The patterns of growth were similar across treatments for body weight and spiral growth as well. All means were calculated on pooled site data. The standard error bars in these diagrams represent the standard error among sites.


Final shell length/initial length
Replicate 1
Replicate 2
A
2.5
2
1.5
Fed 33%
Fed 67%
Fed 100%

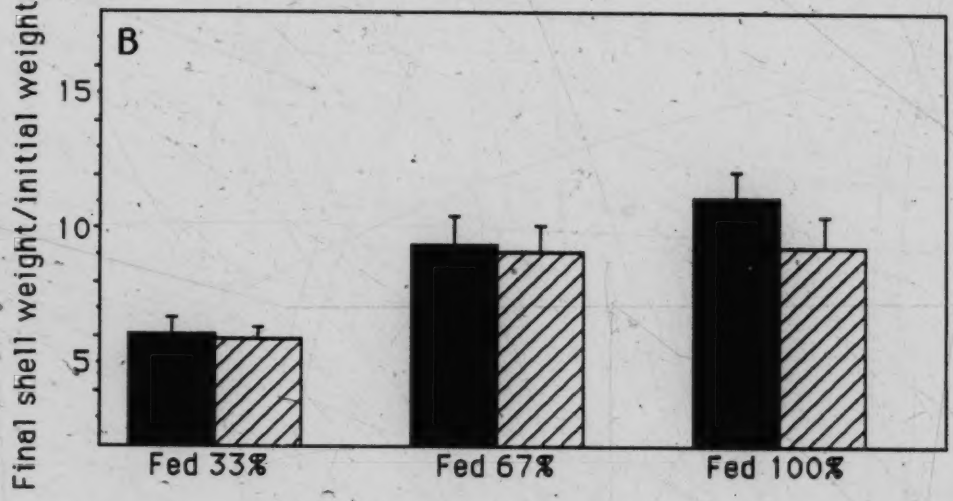
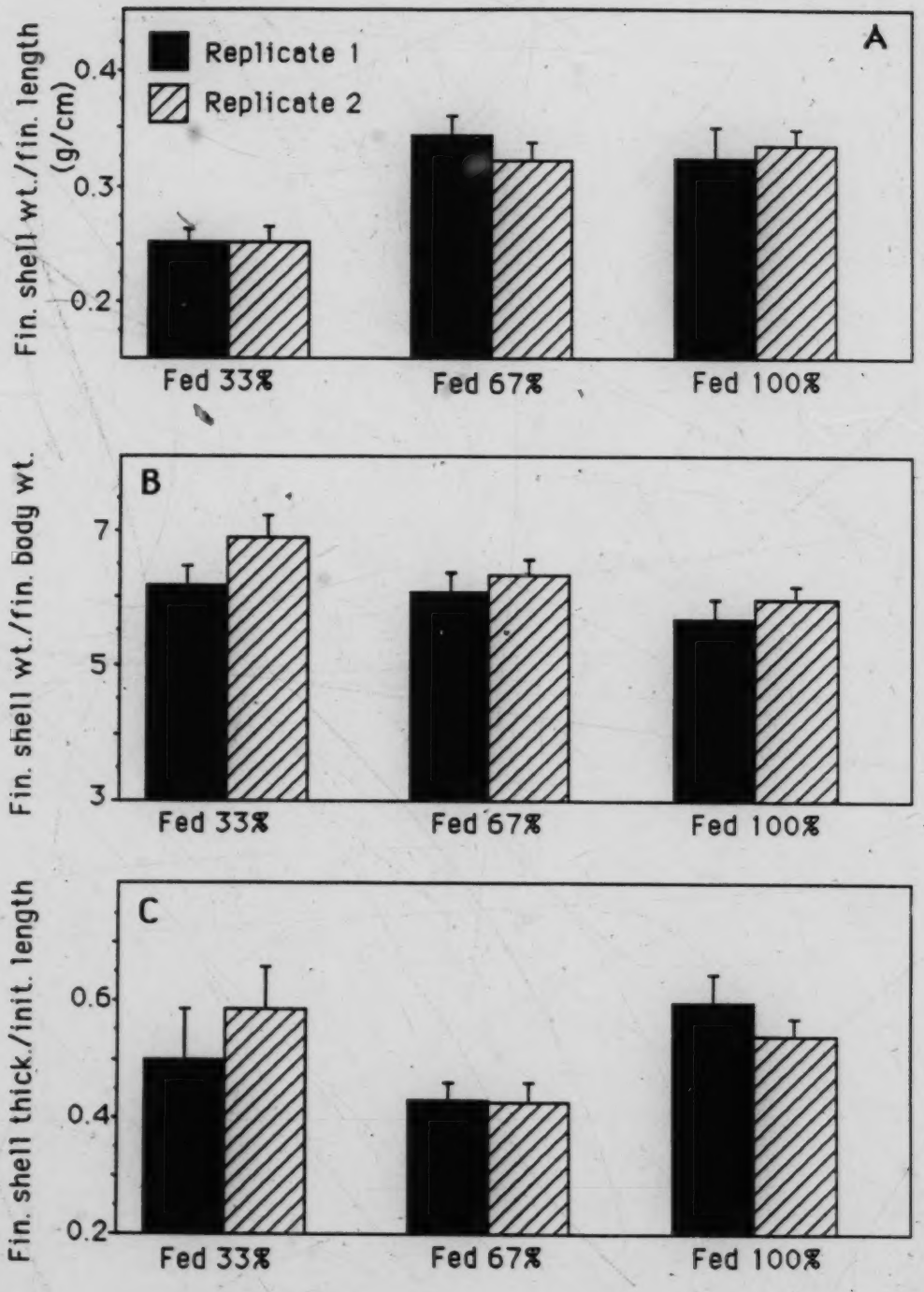

Final shell weight/initial weight
B
15
10
5
Fed 33%
Fed 67%
Fed 100%

Table II - 9. Tests for differences among food availability treatments using results from two-way ANOVA analyses of spiral growth, final shell thickness, and translation rate (shell length change/spiral growth) of *Thais lamellosa* juveniles raised in the absence of crabs and at ambient water temperature (9-11°C). The data are summarized in Table II-2, Figures II-4,5; A4-4,5,6.df = degrees of freedom, MS = mean square, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-value for the site term was calculated by dividing its MS by the MS of the site-replicate term. Similarly, the food MS and the site-food interction MS were divided by the MS for the food-replicate interaction and the site-food-replicate interaction MS, respectively. The remaining MS terms were divided by the error MS to calculate their F-values.

Factor	Spiral growth			Shell thickness			Translation rate		
	df	MS	P	df	MS	P	df	MS	P
Site (A)	4	0.118	0.19	1	0.010	0.51	4	0.124	0.10
Food availability (B)	2	1.885	0.01	2	0.054	0.02	2	0.365	0.03
AB	8	0.038	0.45	2	0.021	0.30	8	0.021	0.67
Replicate (C)	1	0.062	0.12	1	0.000	0.93	1	0.000	0.91
AC	4	0.046	0.18	1	0.000	0.88	4	0.031	0.28
BC	2	0.023	0.45	2	0.001	0.97	2	0.011	0.64
ABC	8	0.035	0.29	2	0.009	0.79	8	0.029	0.30
Error	282	0.029		19	0.037		280	0.024	

Figure II-5.

Differences in final shell morphologies of snails from the food availability experiment. All sites were pooled, and the means were calculated on the pooled data. The standard error bars in these diagrams represent standard error among sites. A = shell weight/shell length, B = shell weight/body weight, C = shell thickness/initial shell length.


A
Replicate 1
Replicate 2
Fin. shell wt./fin. length (g/cm)
0.4
0.3
0.2
Fed 33%
Fed 67%
Fed 100%
B
Fin. shell wt./fin. body wt.
7
5
3
Fed 33%
Fed 67%
Fed 100%
C
Fin. shell thick./init. length
0.6
0.4
0.2
Fed 33%
Fed 67%
Fed 100%

respectively (Table II-10; Figures II-6,7). Differences were found, however, between the same comparisons of final growth parameters: snails fed 33% appeared to secrete relatively thinner shells with respect to shell length than did those of the 67% and 100% food treatments. An examination of the scattergrams (Figures II-8,9) of these data, however, revealed such differences to be small.

Crab presence.

Both the ANCOVA (Table II-11) and the ANOVA (Table II-12) results of final versus initial shell length, shell weight, body weight (Figures II-10; A4-7,8,9) revealed little variation between crab treatments in snails raised with 33% food availability. The ANCOVA results, however (Table II-11; means Table II-2), indicated snails raised with 100% food had significantly reduced growth in shell length (Figure II-10) and body weight in the presence of crabs. Of these latter snails, two sites exhibited reduced growth in shell weight, while no significant difference was found in this measurement in snails from the remaining three sites. The ANOVA results of these same data (Table II-12; means Table II-2; Figure II-10) showed decreased growth in shell length and body weight, but no significant difference in shell weight between crab treatments. Snails of replicate two, fed 33%, increased in shell weight, and decreased in body weight over snails of replicate one. Similarly, replicate two snails fed 100%, increased significantly in shell weight and decreased in body weight over those of replicate one. These results are assumed to be a response due to the higher rate of field-collected snail consumption by the crabs of replicate two.

Table II-10. Tests for differences among food availability treatments using adjusted means from ANCOVA analyses of the logged values of dry shell weight with respect to shell length and dry body weight of *Thais lamellosa* juveniles raised in the absence of crabs, at ambient water temperature (9-11°C). The data are summarized in Figures II-4,5,6,7,8. Y = adjusted mean, SE = standard error, $P < 0.05$ indicates a significant difference at a 95% confidence level in slopes or adjusted means. Initial shell weight was used a secong covariate for the final shell weight comparisons

Axes	Site	Food availability						Common slope		Slope equality	Adjusted means
		Fed 33 %		Fed 67 %		Fed 100 %					
		Y	SE	Y	SE	Y	SE	Slope	SE	(P)	(P)
x = Log initial shell length (cm)	Argyle Crk.	-0.983	0.0120	-0.994	0.0110	-0.994	0.0110	2.706	0.057	0.0021	0.7630
	Aguilar Pt.	-0.977	0.0100	-0.977	0.0089	-0.986	0.0096	2.885	0.060	0.1790	0.4610
y = Log initial shell weight (g)	Cattle Pt.	-1.089	0.0075	-1.091	0.0075	-1.086	0.0075	2.754	0.045	0.0031	0.8840
	Mar Vista	-1.119	0.0089	-1.097	0.0091	-1.118	0.0089	2.800	0.036	0.9800	0.1470
	Sanford Is.	-1.042	0.0100	-1.022	0.0110	-1.030	0.0100	2.759	0.057	0.2510	0.4200
x = Log initial body weight (g)	Argyle Crk.	-1.004	0.0230	-0.964	0.0200	-1.009	0.0200	0.917	0.038	0.8490	0.2480
	Aguilar Pt.	-0.996	0.0180	-0.995	0.0160	-0.965	0.0170	0.912	0.034	0.3030	0.3460
y = Log initial shell weight (g)	Cattle Pt.	-1.095	0.0110	-1.084	0.0110	-1.088	0.0110	0.991	0.023	0.8270	0.7840
	Mar Vista	-1.126	0.0140	-1.084	0.0140	-1.123	0.0140	1.004	0.020	0.0490	0.0590
	Sanford Is.	-1.033	0.0110	-1.012	0.0120	-1.049	0.0110	0.977	0.022	0.4670	0.0840
x = Log final shell length (cm)	Argyle Crk.	-0.176	0.0180	-0.067	0.0140	-0.061	0.0160	1.852	0.187	0.0005	0.0000
	Aguilar Pt.	-0.158	0.0120	-0.102	0.0099	-0.106	0.0110	2.235	0.110	0.6020	0.0032
y = Log final shell weight (g)	Cattle Pt.	-0.136	0.0078	-0.144	0.0072	-0.154	0.0071	2.503	0.080	0.5070	0.2860
	Mar Vista	-0.179	0.0091	-0.149	0.0082	-0.170	0.0076	2.348	0.096	0.0032	0.0560
	Sanford Is.	-0.164	0.0093	-0.157	0.0076	-0.144	0.0093	2.438	0.097	0.1660	0.0430
x = Log final body weight (g)	Argyle Crk.	-0.213	0.0230	-0.089	0.0190	-0.048	0.0200	0.434	0.064	0.0000	0.0000
	Aguilar Pt.	-0.127	0.0160	-0.099	0.0120	-0.137	0.0140	0.685	0.042	0.8640	0.0860
y = Log final shell weight (g)	Cattle Pt.	-0.147	0.0120	-0.137	0.0110	-0.150	0.0110	0.713	0.036	0.0850	0.0860
	Mar Vista	-0.183	0.0140	-0.140	0.0120	-0.175	0.0110	0.715	0.046	0.0190	0.0450
	Sanford Is.	-0.182	0.0140	-0.171	0.0120	-0.121	0.0140	0.590	0.040	0.0000	0.0160

Figure II-6.

Scattergrams of initial shell weight (g) versus initial shell length (cm) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities.

◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

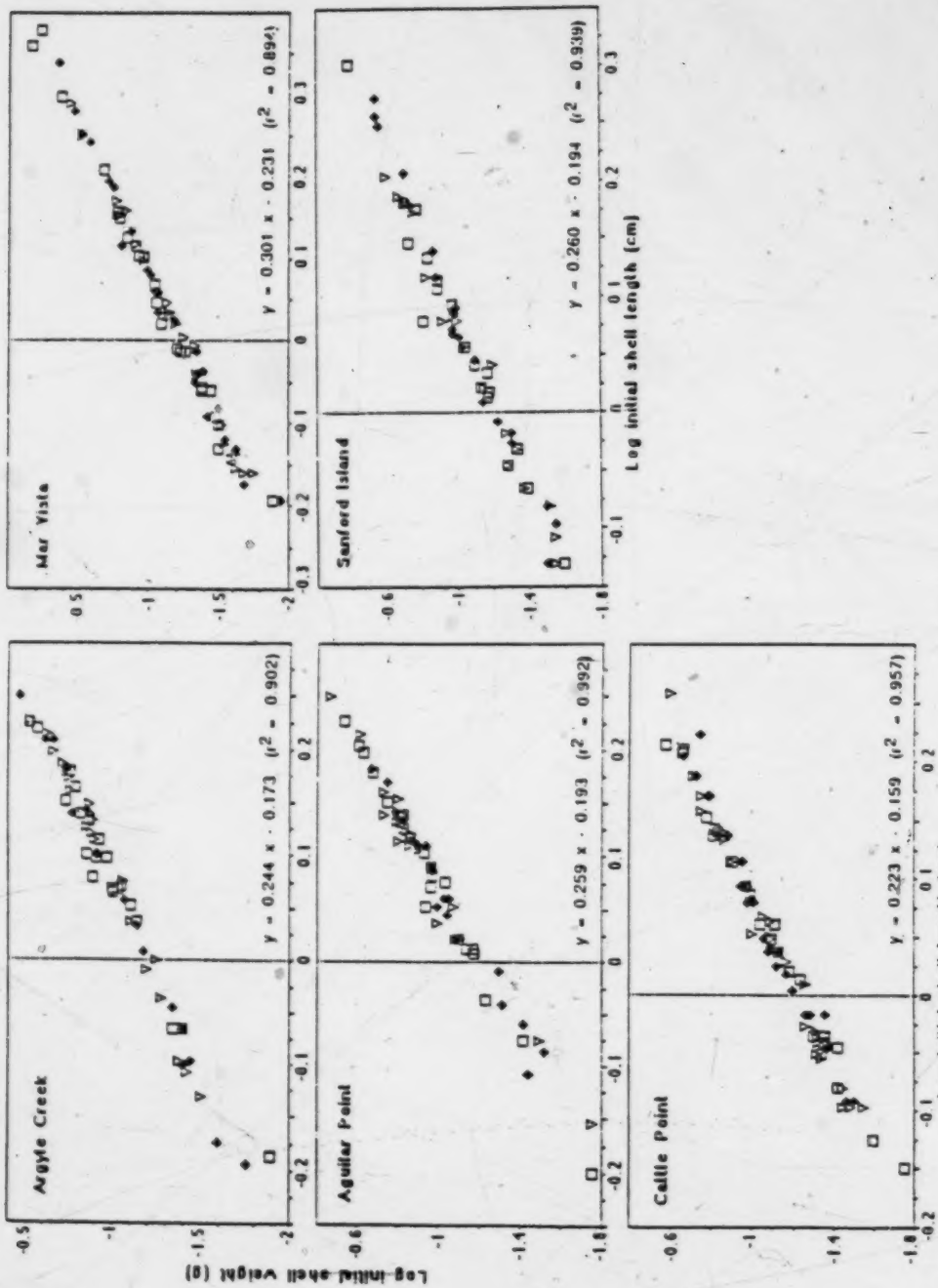

Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point
Log initial shell weight (g)
Log initial shell length (cm)

Figure II-7.

Scattergrams of initial shell weight (g) versus initial body weight (g) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities.

◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

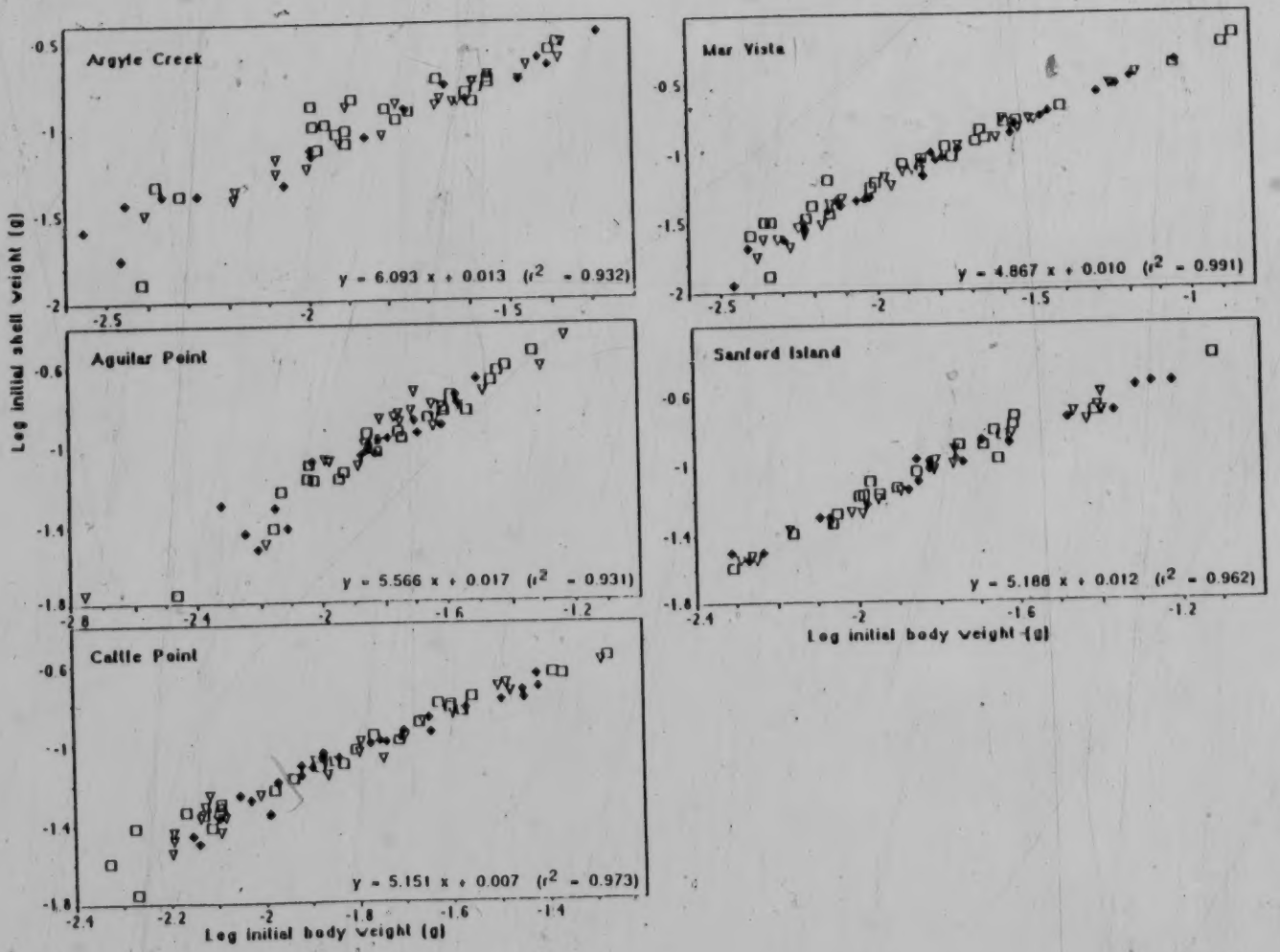

Argyle Creek
y = 6.093 x + 0.013 (r2 = 0.932)
Mar Vista
y = 4.867 x + 0.010 (r2 = 0.991)
Aguilar Point
y = 5.566 x + 0.017 (r2 = 0.931)
Sanford Island
y = 5.188 x + 0.012 (r2 = 0.962)
Cattle Point
y = 5.151 x + 0.007 (r2 = 0.973)
Log initial shell weight (g)
Log initial body weight (g)

Figure II-8.

Scattergrams of final shell weight (g) versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

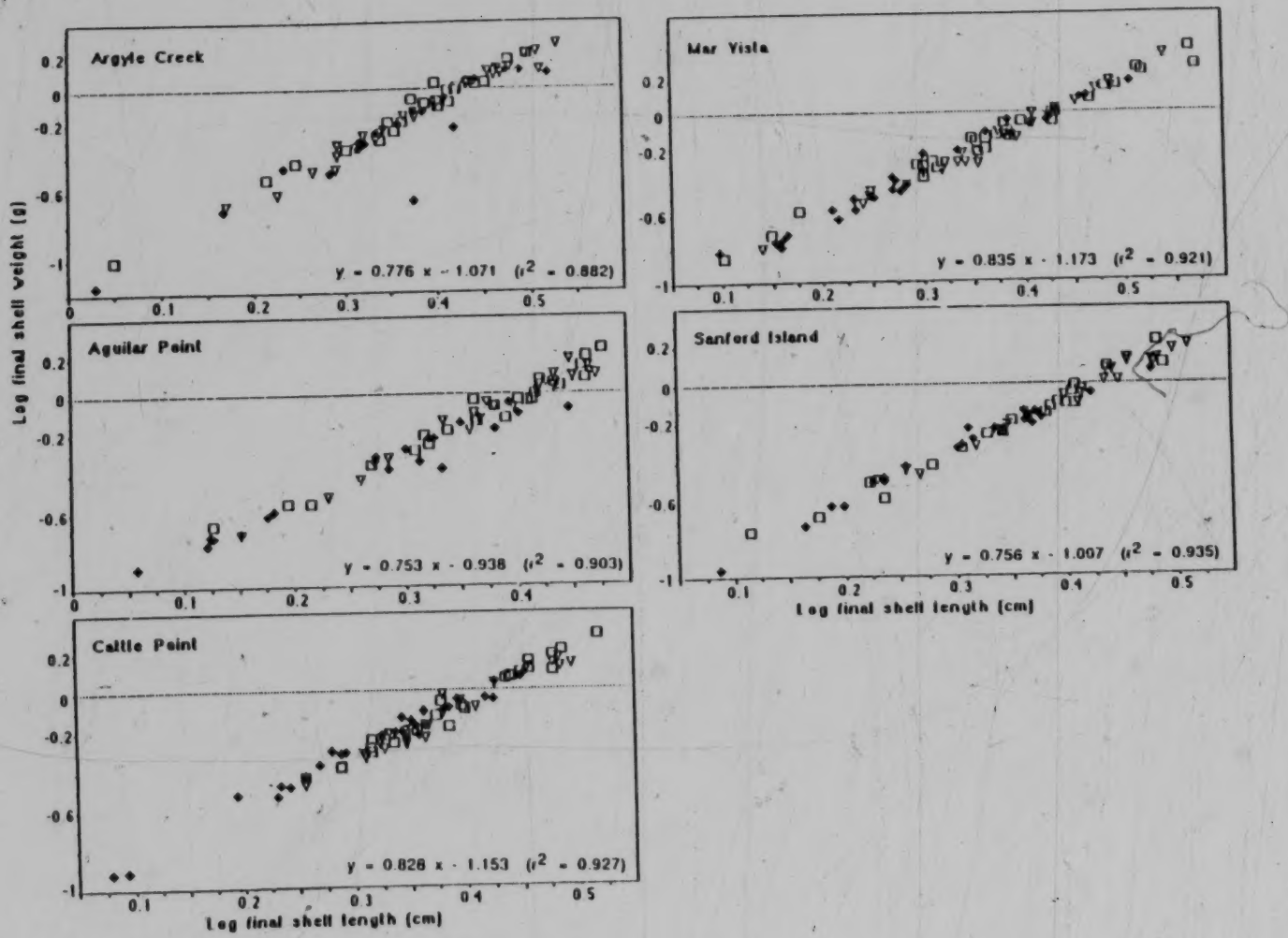

Argyle Creek
y = 0.776 x - 1.071 (r2 = 0.882)
Mar Vista
y = 0.835 x - 1.173 (r2 = 0.921)
Aguilar Point
y = 0.753 x - 0.938 (r2 = 0.903)
Sanford Island
y = 0.756 x - 1.007 (r2 = 0.935)
Cattle Point
y = 0.828 x - 1.153 (r2 = 0.927)
Log final shell weight (g)
Log final shell length (cm)

Figure II-9.

Scattergrams of final dry shell weight (g) versus final dry body weight (g) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities.

◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

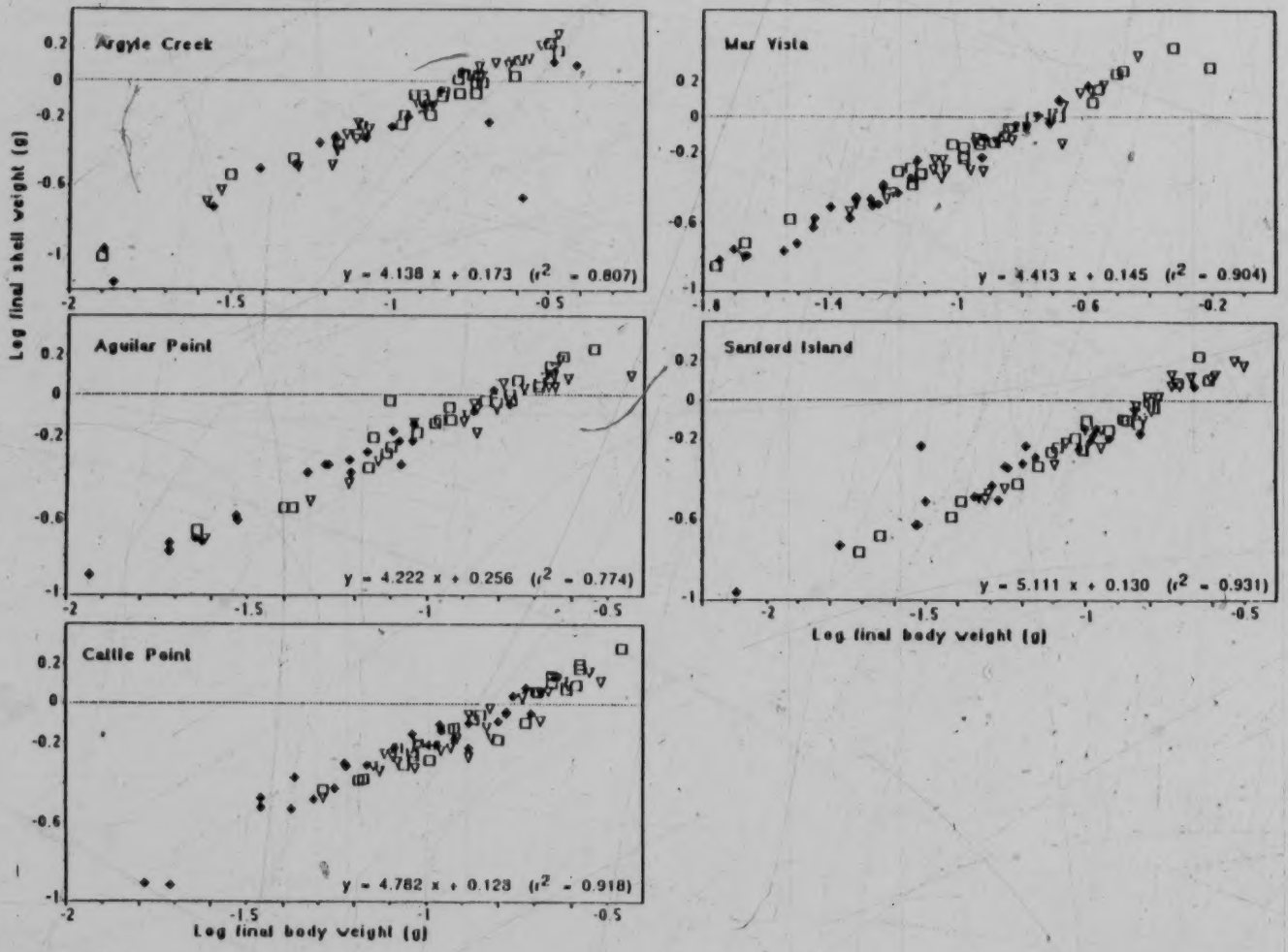

Argyle Creek
y = 4.138 x + 0.173 (r2 = 0.807)
Mar Vista
y = 4.413 x + 0.145 (r2 = 0.904)
Aguilar Point
y = 4.222 x + 0.256 (r2 = 0.774)
Sanford Island
y = 5.111 x + 0.130 (r2 = 0.931)
Cattle Point
y = 4.782 x + 0.128 (r2 = 0.918)
Log final shell weight (g)
Log final body weight (g)

Table II - 11: Tests for differences between crab exposure treatments using adjusted means from ANCOVA analyses of the logged values of initial versus final shell and body parameters of *Thais lamellosa* juveniles raised at two food availabilities and at ambient water temperature (9-11°C). The data are summarized in Table II-2, Figures II-9;A4-7,8,9. Y = adjusted mean, SE = standard error, P≤ 0.05 indicates a significant difference at a 95% confidence level in slopes or adjusted means.

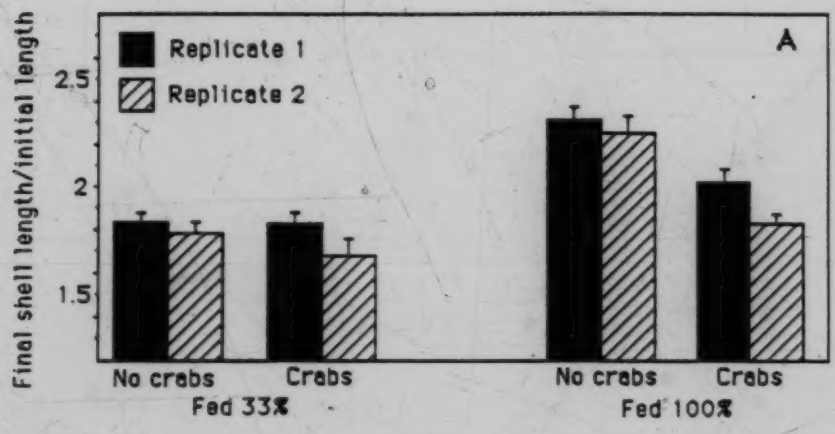
Measurement	Food	Site	Crab Presence				Common slope		Slope equality	Adjusted means
			No Crabs		Crabs					
			Y	SE	Y	SE	Slope	SE	(P)	(P)
Log shell length (cm)	Fed 33%	Argyle Crk.	0.363	0.014	0.319	0.012	0.732	0.090	0.2500	0.0210
		Aguilar Pt.	0.287	0.017	0.256	0.018	0.867	0.128	0.4910	0.2210
		Cattle Pt.	0.315	0.013	0.315	0.013	0.732	0.101	0.5120	0.9960
		Mar Vista	0.305	0.008	0.296	0.009	0.737	0.045	0.6960	0.4840
		Sanford Is.	0.307	0.018	0.234	0.017	0.645	0.110	0.6340	0.0050
Log shell weight (g)	Fed 33%	Argyle Crk.	-0.243	0.033	-0.194	0.029	0.899	0.073	0.3560	0.2670
		Aguilar Pt.	-0.299	0.042	-0.285	0.042	0.813	0.101	0.9640	0.8150
		Cattle Pt.	-0.248	0.039	-0.187	0.041	0.697	0.121	0.2900	0.2900
		Mar Vista	-0.297	0.027	-0.208	0.028	0.754	0.048	0.5640	0.0290
		Sanford Is.	-0.297	0.041	-0.384	0.041	0.813	0.096	0.1440	0.0290
Log body weight (g)	Fed 33%	Argyle Crk.	-1.034	0.063	-1.037	0.055	0.767	0.127	0.6570	0.9740
		Aguilar Pt.	-1.242	0.056	-1.306	0.055	0.943	0.152	0.6230	0.4320
		Cattle Pt.	-1.077	0.045	-1.142	0.047	0.624	0.141	0.0620	0.3260
		Mar Vista	-1.159	0.031	-1.130	0.032	0.799	0.058	0.7370	0.5290
		Sanford Is.	-1.236	0.060	-1.241	0.060	0.839	0.140	0.0380	0.9510
Log shell length (cm)	Fed 100%	Argyle Crk.	0.405	0.013	0.328	0.014	0.500	0.087	0.7280	0.0005
		Aguilar Pt.	0.387	0.013	0.361	0.012	0.623	0.108	0.1630	0.6730
		Cattle Pt.	0.377	0.010	0.339	0.010	0.421	0.075	0.2520	0.0130
		Mar Vista	0.375	0.009	0.329	0.009	0.572	0.049	0.1500	0.0009
		Sanford Is.	0.416	0.011	0.338	0.011	0.595	0.069	0.0640	0.0000
Log shell weight (g)	Fed 100%	Argyle Crk.	-0.061	0.033	-0.147	0.035	0.605	0.081	0.4450	0.0850
		Aguilar Pt.	-0.038	0.034	0.006	0.034	0.635	0.103	0.4700	0.3600
		Cattle Pt.	-0.122	0.028	-0.092	0.028	0.473	0.071	0.4870	0.4440
		Mar Vista	-0.137	0.025	-0.113	0.024	0.605	0.046	0.1790	0.4810
		Sanford Is.	-0.018	0.031	-0.126	0.032	0.653	0.065	0.0023	0.0190
Log body weight (g)	Fed 100%	Argyle Crk.	-0.840	0.053	-1.080	0.058	0.437	0.127	0.2280	0.0060
		Aguilar Pt.	-0.859	0.048	-0.958	0.047	0.690	0.136	0.4580	0.1710
		Cattle Pt.	-0.898	0.039	-1.027	0.039	0.402	0.101	0.1570	0.0260
		Mar Vista	-0.921	0.035	-1.023	0.035	0.701	0.074	0.0550	0.0460
		Sanford Is.	-0.846	0.042	-1.026	0.043	0.710	0.099	0.0014	0.0052

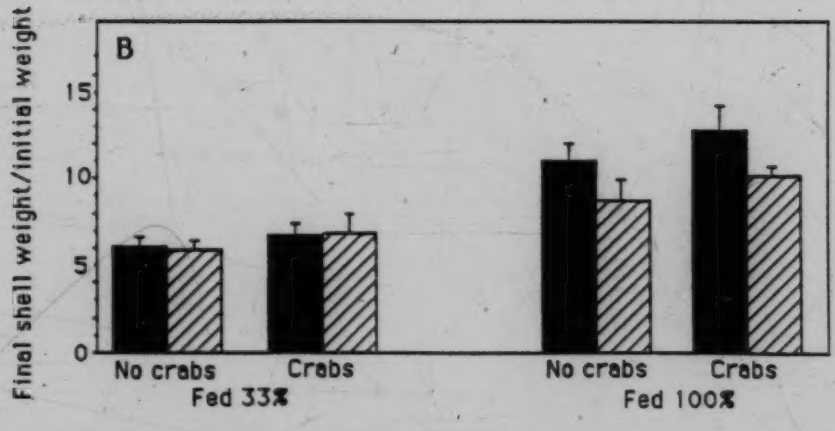
Table II - 12. Tests for differences between crab exposure treatments using results from three-way nested ANOVAs of final over initial shell and body growth parameters of *Thais lamellosa* juveniles raised at two food availabilities and ambient water temperature (9-11°C). The data are summarized in Table II-2, Figures II-9; A4-7,8,9. df = degrees of freedom, MS = mean squares, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-values for the Site, Crab, and Site-Crab Interaction terms were calculated by dividing their respective MS values by the Replicate MS. The Replicate F- value was calculated by dividing the Replicate MS by the Error MS.

Food avail.	Factors	df	Final shell length/ initial shell length		Final shell weight/ initial shell weight		Final body weight/ initial body weight	
			MS	P	MS	P	MS	P
Fed 33 %	Site	4	0.013	0.12	0.146	0.12	0.240	0.23
	Crab presence	1	0.017	0.11	0.028	0.51	0.001	0.93
	Interaction	4	0.006	0.40	0.041	0.63	0.032	0.92
	Replicate	10	0.006	0.14	0.061	0.01	0.141	0.00
	Error	174	0.005		0.026		0.032	
Fed 100 %	Site	4	0.003	0.93	0.111	0.42	0.064	0.93
	Crab presence	1	0.292	0.001	0.070	0.43	3.475	0.01
	Interaction	4	0.009	0.66	0.128	0.36	0.079	0.90
	Replicate	10	0.015	0.03	0.104	0.13	0.300	0.00
	Error	196	0.005		0.036		0.053	

Figure II-10.

Relative growth in shell length (A) and shell weight (B) of snails from the crab-exposure experiment. The patterns of growth in shell length were similar across treatments to body weight and spiral growth. All sites were pooled, and the means were calculated on the pooled data. The standard error bars in these diagrams represent the standard errors among sites.


Replicate 1
Replicate 2
A
Final shell length/initial length
2.5
2
1.5
No crabs
Crabs
Fed 33%
No crabs
Crabs
Fed 100%


B
Final shell weight/initial weight
15
10
5
0
No crabs
Crabs
Fed 33%
No crabs
Crabs
Fed 100%

Snails raised with both 33 and 100% food availabilities showed a decrease in spiral growth and an increase in shell thickness when maintained in the presence of crabs (Table II-13; Figures A4-10,11,12). Translation rate appeared to be significantly different with respect to the site-crab interaction term, but the scattergrams (Figure A4-17) of these data demonstrated no correlation between translation rate and site. This apparent change in translation rate, however, is probably an artifact due to spiral shell growth rate differences (Figure A4-12). No significant difference was found between sites in snails of the 100% food category, and although the ANOVA results indicated significant differences between sites with respect to shell thickness at a 93% confidence level in snails of 33% food, the scattergrams of these data (Figure A4-16) indicate differences between sites to be small.

Final shell weight was significantly higher with respect to final shell length and final body weight in snails raised in the presence of crabs (Figure II-11). Pre-experimental values, however, also demonstrated this trend (ANOVA Table II-14), but when final values were re-tested with initial shell weight as a covariate, significant results were still obtained with the final values (ANOVA Table II-14, Figures II-12,13,14,15), with the exception of snails from Sanford Island, raised with 33% food. An explanation for this variation in pre-experimental data could lie in the fact that due to the duration of the measurement time, the crab-presence individuals were exposed to crabs for a period of up to three days before being measured.

Table II - 13. Tests for differences between crab exposure treatments using results from two-way ANOVAs of spiral growth, final shell thickness, and translation rate (shell length change/spiral growth) of *Thais lamellosa* juveniles raised at two food availabilities and at ambient water temperature (9-11°C). The data are summarized in Table II-2, Figures II-10,11; A4-10,11,12.df = degrees of freedom, MS = mean squares, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-values for the Site, Crab, and Site-Crab Interaction terms were calculated by dividing their respective MS values by the Replicate MS. The Replicate F- value was calculated by dividing the Replicate MS by the Error MS.

Food avail.	Factor	Spiral growth			Shell thickness			Translation rate		
		df	MS	P	df	MS	P	df	MS	P
Fed 33%	Site	4	0.038	0.27				4	0.007	0.79
	Crab	1	1.297	0.00	1	0.305	0.14	1	0.212	0.005
	Interaction	4	0.159	0.01				4	0.098	0.01
	Replicate	10	0.022	0.77	2	0.053	0.09	10	0.016	0.76
	Error	172	0.034		13	0.018		168	0.024	
Fed 100%	Site	4	0.062	0.89	4	0.015	0.90	4	0.038	0.75
	Crab	1	1.106	0.05	1	0.795	0.004	1	0.090	0.31
	Interaction	4	0.053	0.92	4	0.008	0.72	4	0.078	0.00
	Replicate	10	0.234	0.00	10	0.051	0.004	10	0.078	0.00
	Error	221	0.025		39	0.018		190	0.024	

Figure II-11.

Differences in final shell morphology of snails from the crab-exposure experiment. All sites were pooled, and the means were calculated on the pooled data. The standard error bars in the diagrams represent the standard error among sites. A = shell weight/shell length, B = shell weight/body weight, C = shell thickness/ initial shell length.

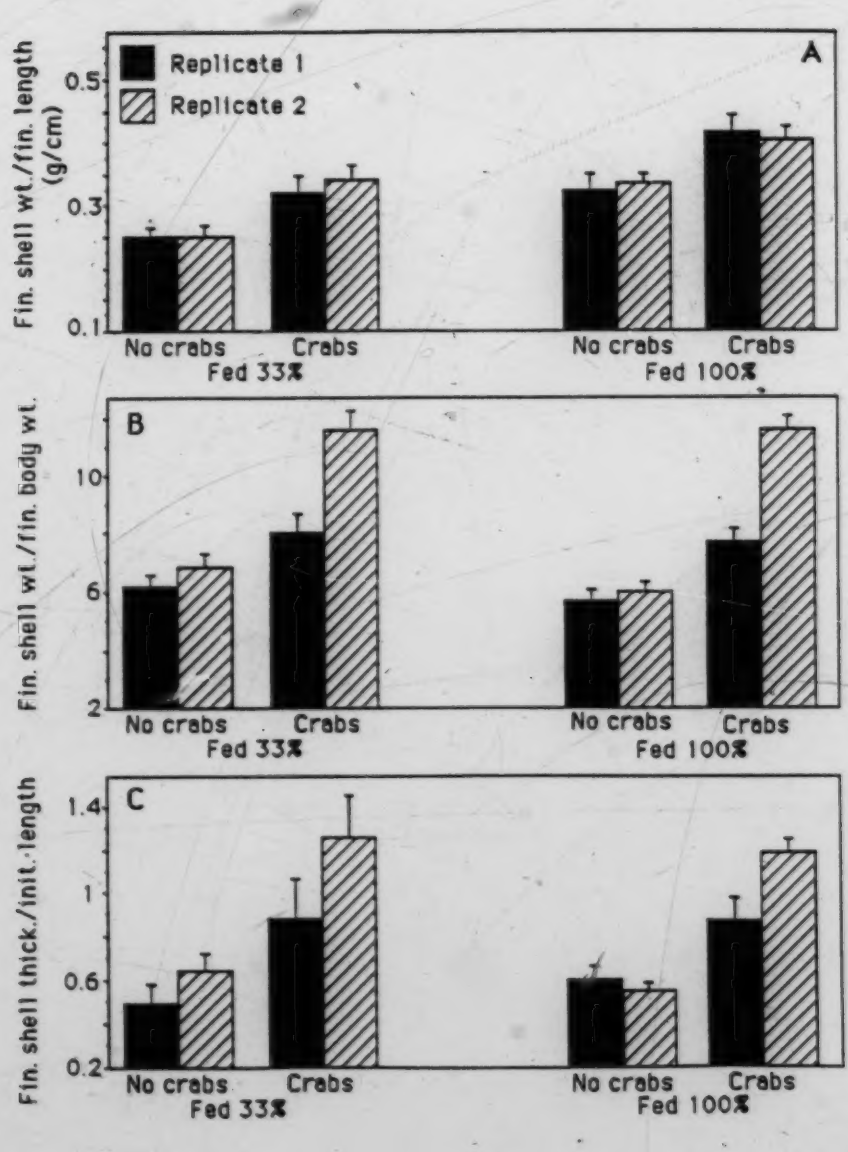

Replicate 1
Replicate 2
A
Fin. shell wt./fin. length (g/cm)
0.5
0.3
0.1
No crabs
Crabs
Fed 33%
No crabs
Crabs
Fed 100%
B
Fin. shell wt./fin. body wt.
10
6
2
No crabs
Crabs
Fed 33%
No crabs
Crabs
Fed 100%
C
Fin. shell thick./init. length
1.4
1
0.6
0.2
No crabs
Crabs
Fed 33%
No crabs
Crabs
Fed 100%

Table II - 14. Tests for differences between crab exposure treatments using adjusted means from ANCOVA analyses of the logged values of dry shell weight with respect to shell length and dry body weight of *Thais lamellosa* juveniles reared at two food availabilities, at ambient water temperature (9-11°C). The data are summarized in Figures II-10, 11, 12, 13, 14. Y = adjusted mean, SE = standard error, $P \leq 0.05$ indicates a significant difference at a 95% confidence level in slopes or adjusted means. Initial shell weight was used as a second covariate for the final shell weight comparisons.

Axes	Food availability	Site	Crab presence				Common slope		Slope equality	Adjusted means
			No crabs		Crabs					
			Y	SE	Y	SE	Slope	SE	(P)	(P)
x = Log initial shell length (cm)	Fed 33 %	Argyle Crk.	-1.017	0.0100	-0.959	0.0091	2.762	0.060	0.0410	0.0001
y = Log initial shell weight (g)		Aguilar Pt.	-1.100	0.0120	-1.015	0.0120	2.999	0.089	0.1730	0.0000
		Cattle Pt.	-1.100	0.0087	-1.072	0.0087	2.758	0.067	0.0460	0.0213
		Mar Vista	-1.134	0.0120	-1.048	0.0120	2.856	0.057	0.4240	0.0000
		Sanford Is.	-1.074	0.0100	-0.998	0.0100	2.830	0.063	0.0026	0.0000
x = Log initial body weight (g)	Fed 33 %	Argyle Crk.	-1.090	0.0220	-0.897	0.0200	0.901	0.045	0.7970	0.0000
y = Log initial shell weight (g)		Aguilar Pt.	-1.115	0.0260	-0.998	0.0270	1.054	0.072	0.0870	0.0043
		Cattle Pt.	-1.115	0.0160	-1.059	0.0160	1.019	0.048	0.4820	0.0200
		Mar Vista	-1.181	0.0180	-0.999	0.0180	1.064	0.033	0.3120	0.0000
		Sanford Is.	-1.106	0.0190	-0.968	0.0190	1.034	0.045	0.0270	0.0000
x = Log final shell length (cm)	Fed 33 %	Argyle Crk.	-0.263	0.0260	-0.131	0.0210	1.822	0.303	0.0024	0.0002
y = Log final shell weight (g)		Aguilar Pt.	-0.377	0.0170	-0.207	0.0170	2.452	0.186	0.0066	0.0000
		Cattle Pt.	-0.259	0.0340	-0.172	0.0370	1.842	0.468	0.2850	0.0950
		Mar Vista	-0.336	0.0110	-0.165	0.0110	2.658	0.170	0.0007	0.0000
		Sanford Is.	-0.363	0.0390	-0.319	0.0380	1.453	0.339	0.0220	0.4650
x = Log final body weight (g)	Fed 33 %	Argyle Crk.	-0.277	0.0280	-0.168	0.0240	0.354	0.085	0.0022	0.0081
y = Log final shell weight (g)		Aguilar Pt.	-0.378	0.0130	-0.224	0.0130	0.723	0.042	0.0720	0.0000
		Cattle Pt.	-0.287	0.0190	-0.144	0.0200	0.829	0.066	0.0460	0.0000
		Mar Vista	-0.339	0.0190	-0.162	0.0190	0.781	0.103	0.2160	0.0000
		Sanford Is.	-0.323	0.0350	-0.358	0.0350	0.410	0.097	0.1960	0.5010
x = Log initial shell length (cm)	Fed 100 %	Argyle Crk.	-1.051	0.0110	-0.994	0.0120	2.649	0.071	0.0260	0.0015
y = Log initial shell weight (g)		Aguilar Pt.	-0.991	0.0170	-0.904	0.0160	2.925	0.131	0.3550	0.0008
		Cattle Pt.	-1.152	0.0092	-1.088	0.0092	2.819	0.068	0.0120	0.0000
		Mar Vista	-1.187	0.0089	-1.116	0.0084	2.930	0.047	0.0012	0.0000
		Sanford Is.	-1.094	0.0089	-1.018	0.0092	2.936	0.055	0.2130	0.0000
x = Log initial body weight (g)	Fed 100 %	Argyle Crk.	-1.078	0.0270	-0.960	0.0300	0.915	0.064	0.7310	0.0086
y = Log initial shell weight (g)		Aguilar Pt.	-1.013	0.0210	-0.883	0.0200	0.908	0.051	0.1660	0.0001
		Cattle Pt.	-1.205	0.0160	-1.036	0.0160	1.011	0.041	0.3910	0.0000
		Mar Vista	-1.228	0.0230	-1.079	0.0210	1.108	0.046	0.2270	0.0000
		Sanford Is.	-1.136	0.0160	-0.964	0.0170	1.128	0.039	0.0000	0.0000
x = Log final shell length (cm)	Fed 100 %	Argyle Crk.	-0.159	0.0130	-0.031	0.0150	2.495	0.163	0.2170	0.0000
y = Log final shell weight (g)		Aguilar Pt.	-0.103	0.0100	0.067	0.0099	2.647	0.130	0.4190	0.0000
		Cattle Pt.	-0.189	0.0085	-0.028	0.0083	2.714	0.113	0.0760	0.0000
		Mar Vista	-0.219	0.0073	-0.035	0.0071	2.630	0.104	0.1380	0.0000
		Sanford Is.	-0.129	0.0150	-0.009	0.0150	2.509	0.151	0.0036	0.0000
x = Log final body weight (g)	Fed 100 %	Argyle Crk.	-0.143	0.0200	-0.051	0.0230	0.642	0.073	0.0620	0.0110
y = Log final shell weight (g)		Aguilar Pt.	-0.118	0.0160	0.080	0.0150	0.706	0.054	0.7960	0.0000
		Cattle Pt.	-0.193	0.0110	-0.024	0.0110	0.716	0.040	0.1510	0.0000
		Mar Vista	-0.199	0.0130	-0.054	0.0130	0.590	0.049	0.0160	0.0000
		Sanford Is.	-0.109	0.0190	-0.030	0.0200	0.652	0.069	0.0054	0.0150

Figure II-12.

Scattergrams of initial dry shell weight (g) versus initial shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities.

◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

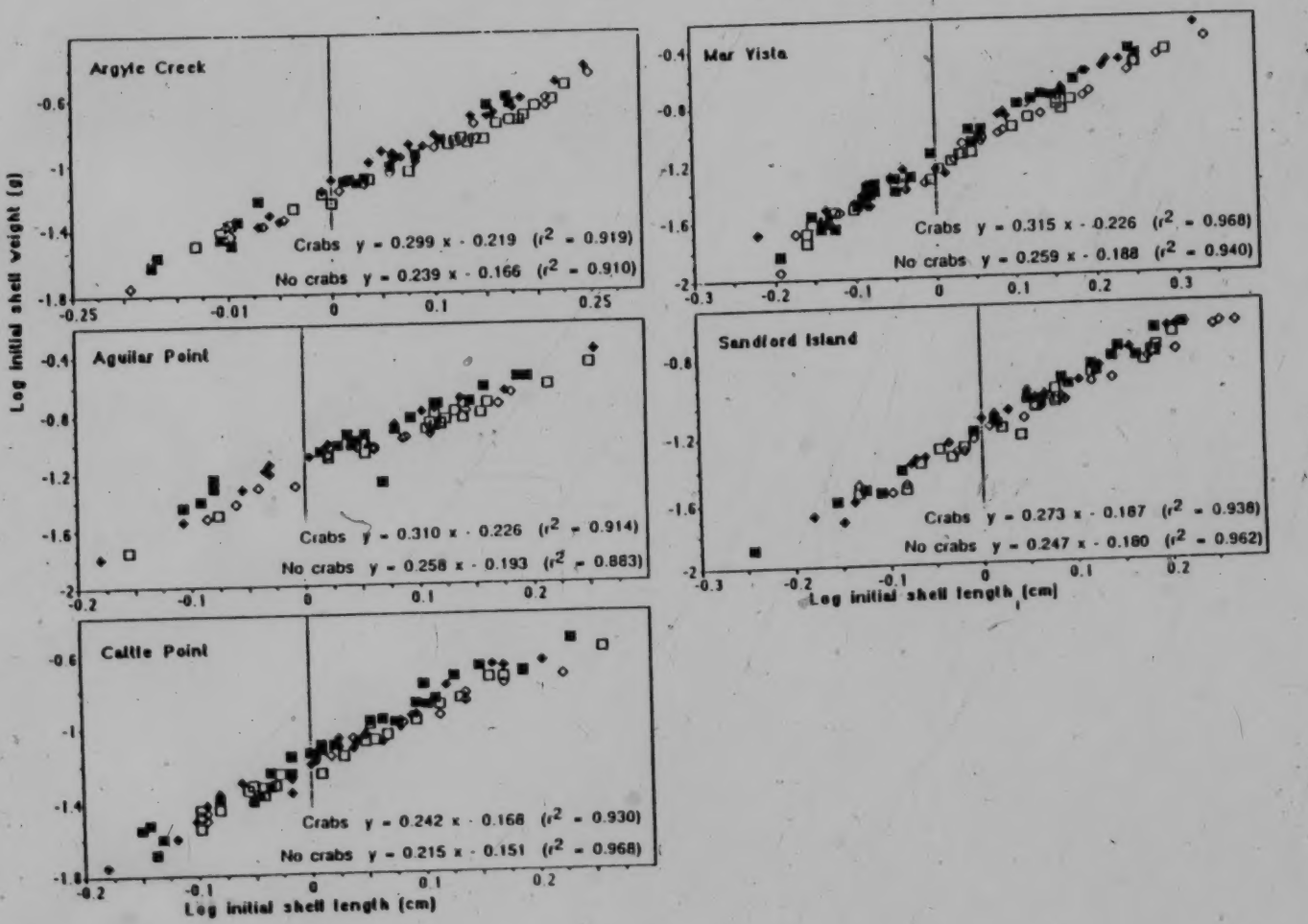

Argyle Creek
Crabs y = 0.299 x - 0.219 (r2 = 0.919)
No crabs y = 0.239 x - 0.166 (r2 = 0.910)
Mar Vista
Crabs y = 0.315 x - 0.226 (r2 = 0.968)
No crabs y = 0.259 x - 0.188 (r2 = 0.940)
Aguilar Point
Crabs y = 0.310 x - 0.226 (r2 = 0.914)
No crabs y = 0.258 x - 0.193 (r2 = 0.883)
Sandford Island
Crabs y = 0.273 x - 0.187 (r2 = 0.938)
No crabs y = 0.247 x - 0.180 (r2 = 0.962)
Cattle Point
Crabs y = 0.242 x - 0.168 (r2 = 0.930)
No crabs y = 0.215 x - 0.151 (r2 = 0.968)
Log initial shell weight (g)
Log initial shell length (cm)

Figure II-13.

Scattergrams of initial dry shell weight (g) versus initial dry body weight (g) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities.

◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs,

■ = fed 100%, crabs.

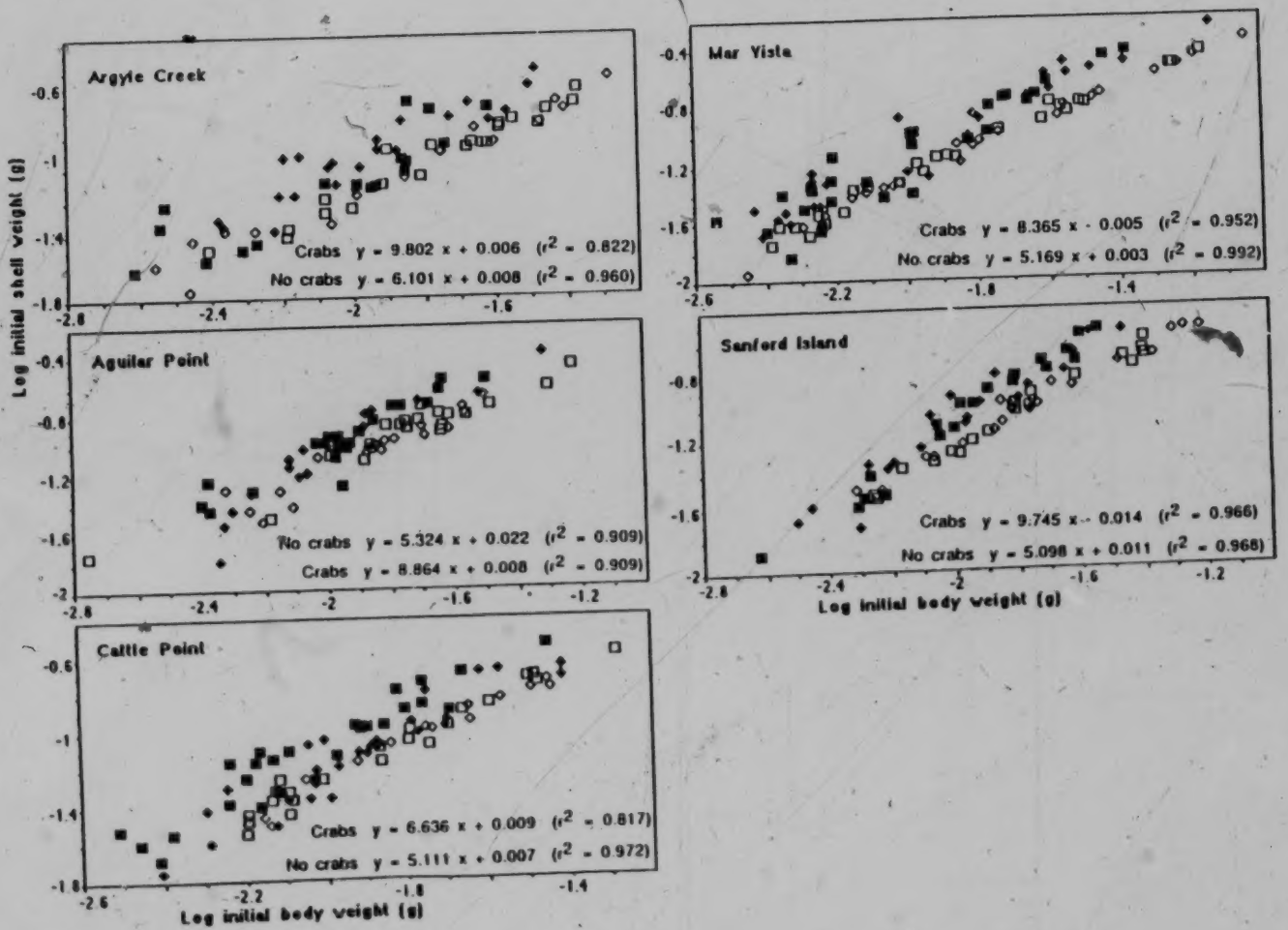

Argyle Creek
Crabs y = 9.802 x + 0.006 (r2 = 0.822)
No crabs y = 6.101 x + 0.008 (r2 = 0.960)
Mar Vista
Crabs y = 8.365 x - 0.005 (r2 = 0.952)
No crabs y = 5.169 x + 0.003 (r2 = 0.992)
Aguilar Point
No crabs y = 5.324 x + 0.022 (r2 = 0.909)
Crabs y = 8.864 x + 0.008 (r2 = 0.909)
Sanford Island
Crabs y = 9.745 x - 0.014 (r2 = 0.966)
No crabs y = 5.098 x + 0.011 (r2 = 0.968)
Cattle Point
Crabs y = 6.636 x + 0.009 (r2 = 0.817)
No crabs y = 5.111 x + 0.007 (r2 = 0.972)
Log initial shell weight (g)
Log initial body weight (g)

Figure II-14.

Scattergrams of final dry shell weight (g) versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities.

◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

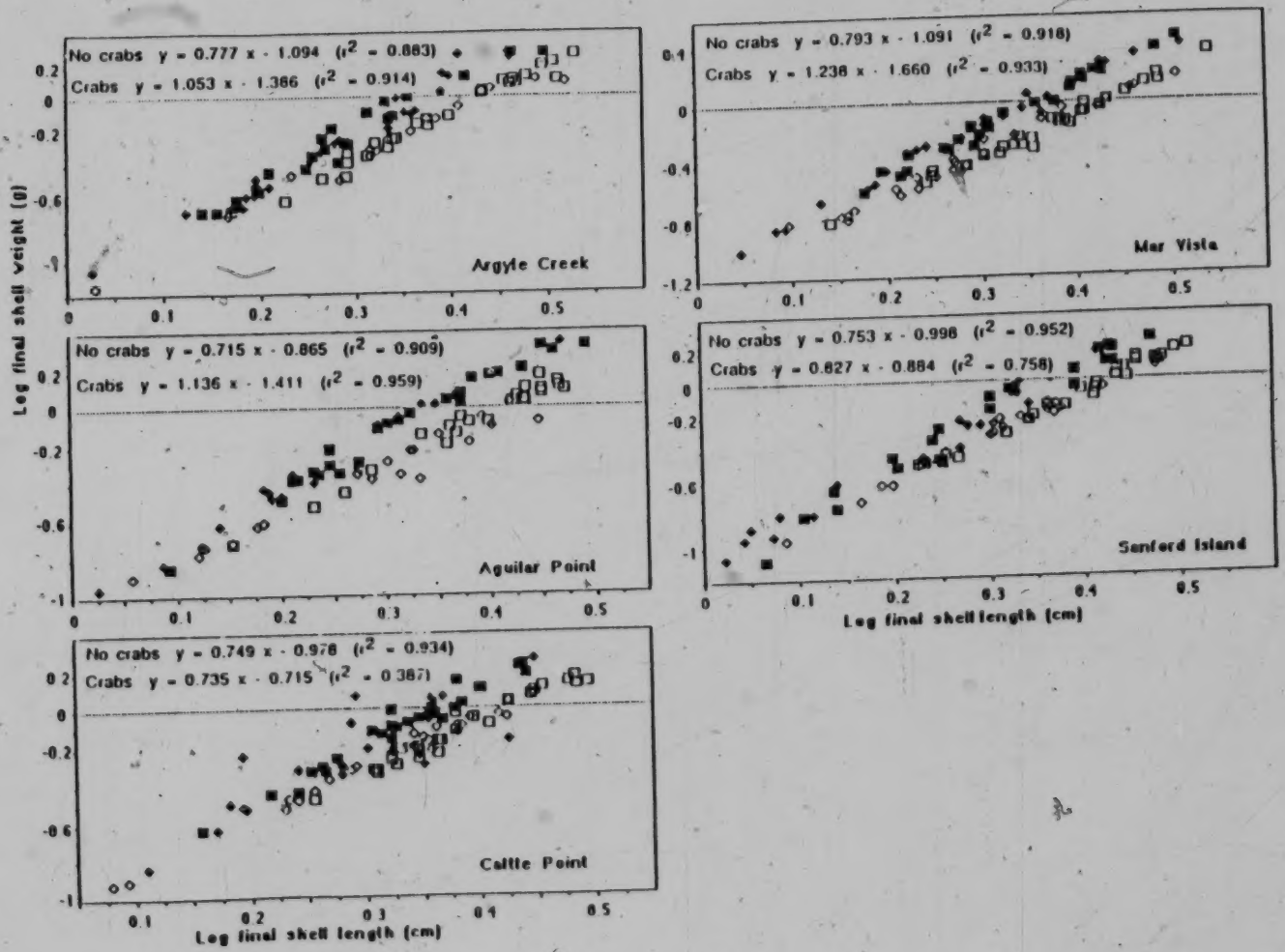
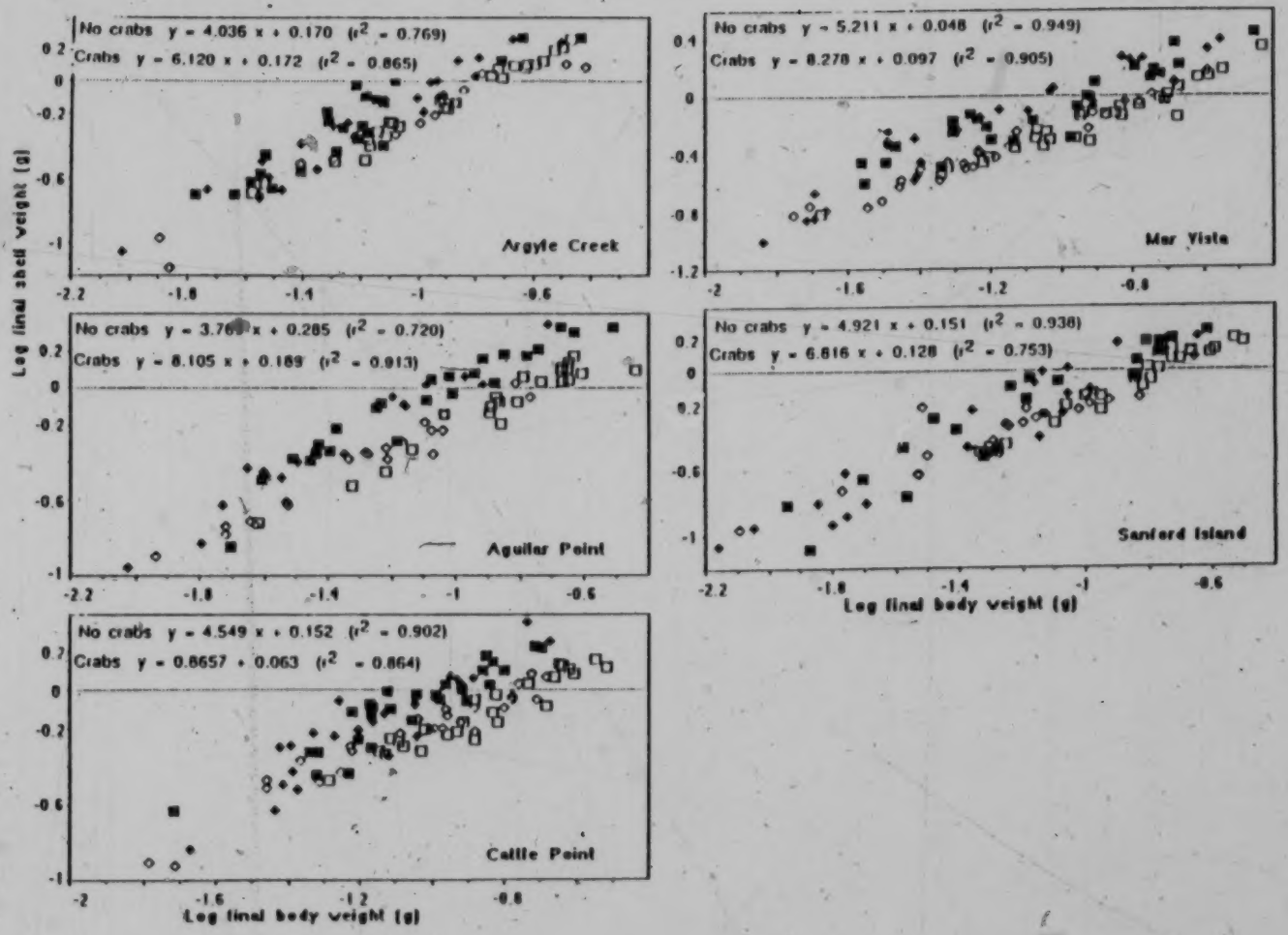

No crabs y = 0.777 x - 1.094 (r2 = 0.883)
Crabs y = 1.053 x - 1.386 (r2 = 0.914)
Argyle Creek
No crabs y = 0.793 x - 1.091 (r2 = 0.918)
Crabs y = 1.238 x - 1.660 (r2 = 0.933)
Mar Vista
No crabs y = 0.715 x - 0.865 (r2 = 0.909)
Crabs y = 1.136 x - 1.411 (r2 = 0.959)
Aguilar Point
No crabs y = 0.753 x - 0.998 (r2 = 0.952)
Crabs y = 0.827 x - 0.884 (r2 = 0.758)
Sanford Island
No crabs y = 0.749 x - 0.978 (r2 = 0.934)
Crabs y = 0.735 x - 0.715 (r2 = 0.387)
Cattle Point
Log final shell weight (g)
Log final shell length (cm)

Figure II-15.

Scattergrams of final dry shell weight (g) versus final dry body weight (g) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the presence and absence of crabs, and at two food availabilities.

◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs,

■ = fed 100%, crabs.


No crabs y = 4.036 x + 0.170 (r2 = 0.769)
Crabs y = 6.120 x + 0.172 (r2 = 0.865)
Argyle Creek
No crabs y = 5.211 x + 0.048 (r2 = 0.949)
Crabs y = 8.278 x + 0.097 (r2 = 0.905)
Mar Vista
No crabs y = 3.769 x + 0.285 (r2 = 0.720)
Crabs y = 8.105 x + 0.189 (r2 = 0.913)
Aguilar Point
No crabs y = 4.921 x + 0.151 (r2 = 0.938)
Crabs y = 6.816 x + 0.128 (r2 = 0.753)
Sanford Island
No crabs y = 4.549 x + 0.152 (r2 = 0.902)
Crabs y = 0.8657 + 0.063 (r2 = 0.864)
Cattle Point
Log final shell weight (g)
Log final body weight (g)

The number of field-collected snails consumed by the experimental crabs differed by approximately a factor of two between replicates (see Table II-15). Snails of replicate two (that replicate of increased crab feeding) showed a higher probability of developing apertural teeth than those of replicate one (Table II-15). Of these snails, those from Argyle Creek showed a significantly lower probability of developing apertural teeth (Table II-16; means Table II-15). No apertural tooth development was noted in snails raised in the absence of crabs.

Temperature.

Both the ANCOVA (Table II-17) and the ANOVA (Table II-18) tests of final versus initial growth measurements (shell length, shell weight, body weight) revealed similar results: snails raised at 15° and 18°C grew at slower rates than did snails raised at ambient sea water temperatures (9-11°C) (Figures II-16; A4-13). Snails raised at ambient sea water temperature increased in spiral growth more rapidly, and secreted thinner shells (Figure II-17) than did snails raised at increased water temperatures (ANOVA Tables II-19,20; Figure A4-14). The site-temperature interaction term appeared to be significant with respect to translation rate, although the scattergrams (Figure A4-20) of these data indicate site differences between treatments were small. No significant difference was found between the 15° and the 18°C treatments.

Results from ANCOVAs for shell weight regressed against shell length and body weight respectively, revealed statistically

Table II - 15: Degree of apertural tooth development in juvenile *Thais lamellosa* raised at two food availabilities and in the presence of crabs. Apertural tooth scoring: 1 = no teeth, 2 to 4 = a gradation of tooth development, with 2 = minimal to 4 = well developed. N = sample size, Mean = mean of scored data

	Fed 33%				Fed 100%			
	Replicate 1		Replicate 2		Replicate 1		Replicate 2	
Site	Mean	N	Mean	N	Mean	N	Mean	N
Argyle Crk.	1.091	11	1.250	12	1.000	9	1.000	11
Aguilar Pt.	1.750	8	2.333	9	1.000	11	1.800	10
Cattle Pt.	1.667	12	2.600	10	1.071	14	1.700	10
Mar Vista	1.500	12	2.333	12	1.000	11	1.600	10
Sanford Is.	1.364	11	2.333	9	1.083	12	1.636	11

Number of field-collected snails consumed by the experimental crabs.

	Fed 33%, 100%	
	Replicate 1	Replicate 2
All sites	49	92

Table II-16. Tests for differences between sites, food availabilities, and replicates with respect to presence vs. absence of apertural teeth, using Chi-square statistics. Only snails from the crab-presence treatments are represented here. Snails from the crab-absence treatments did not develop apertural teeth. df = degrees of freedom, $P \leq 0.05$ indicates a significant difference between factors at a 95% confidence level.

Factor	Apertural tooth development		
	df	Total Chi-square	P
Site	4	19.483	0.0006
Food availability	1	21.836	0.0001
Replicates	1	18.666	0.0001

Table II - 17. Tests for differences among water temperature treatmentsusing adjusted means from ANCOVA analyses of the logged values of initial versus final shell and body parameters of *Thais lamellosa* juveniles raised in the absence of crabs with a 100% food availability. The data are summarized in Table II-3, Figures II-15; A4-13. Y = adjusted mean, SE = standard error, P≤ 0.05 indicates a significant difference at a 95% comfidence level in slopes or adjusted means.

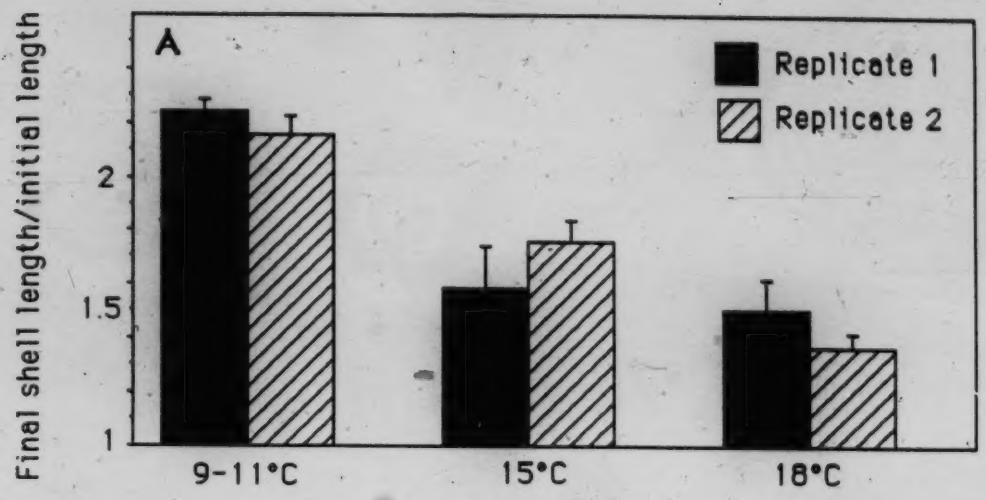
Measurement	Site	Temperature						Common slope		Slope equality	Adjusted means
		Ambient (9-11°C)		15° C		18°C					
		Y	SE	Y	SE	Y	SE	Slope	SE	(P)	(P)
Log shell length (cm)	Argyle Crk.	0.364	0.012	0.270	0.014	0.217	0.011	0.470	0.099	0.0060	0.0000
	Mar Vista	0.378	0.013	0.230	0.018	0.250	0.013	0.606	0.091	0.5840	0.0000
Log shell weight (g)	Argyle Crk.	-0.143	0.012	-0.203	0.014	-0.226	0.012	0.235	0.038	0.0010	0.0001
	Mar Vista	-0.129	0.015	-0.223	0.019	-0.231	0.015	0.267	0.037	0.6150	0.0000
Log body weight (g)	Argyle Crk.	-0.969	0.036	-1.205	0.042	-1.307	0.033	0.464	0.101	0.0060	0.0000
	Mar Vista	-0.906	0.051	-1.328	0.061	-1.380	0.051	0.668	0.114	0.6270	0.0000

Table II - 18. Tests for differences among water temperature treatments using results from two-way ANOVAs of final versus initial shell and body parameters of *Thais lamellosa* juveniles raised in the absence of crabs and with full food availability. The data are summarized in Table II-3, Figures II-15; A4-13. df = degrees of freedom, MS = mean square, $P \leq 0.05$ indicates a significant difference at a 95% confidence level in shell or body parameters. The F-values for the Site, Temperature, and Site-Temperature Interaction terms were calculated by dividing their respective MS values by the Replicate MS. The Replicate F-values were calculated by dividing the Replicate MS by the Error MS.

Factors	df	Final shell length/ initial shell length		Final shell weight/ initial shell weight		Final body weight/ initial body weight	
		MS	P	MS	P	MS	P
Site	1	0.001	0.66	0.004	0.73	0.051	0.35
Temperature	2	0.178	0.001	0.165	0.04	0.985	0.002
Interaction	2	0.005	0.52	0.023	0.48	0.064	0.34
Replicate	6	0.007	0.25	0.027	0.62	0.049	0.52
Error	110	0.005		0.037		0.056	

Figure II-16.

Relative growth in shell length (A) and shell weight (B) of snails from the water temperature experiment. The patterns of growth were similar across treatments for body weight and spiral growth. All sites were pooled, and the means were calculated on the pooled data. The standard error bars of these diagrams represent the standard error between sites.


A
Replicate 1
Replicate 2
Final shell length/initial length
2
1.5
1
9-11°C
15°C
18°C

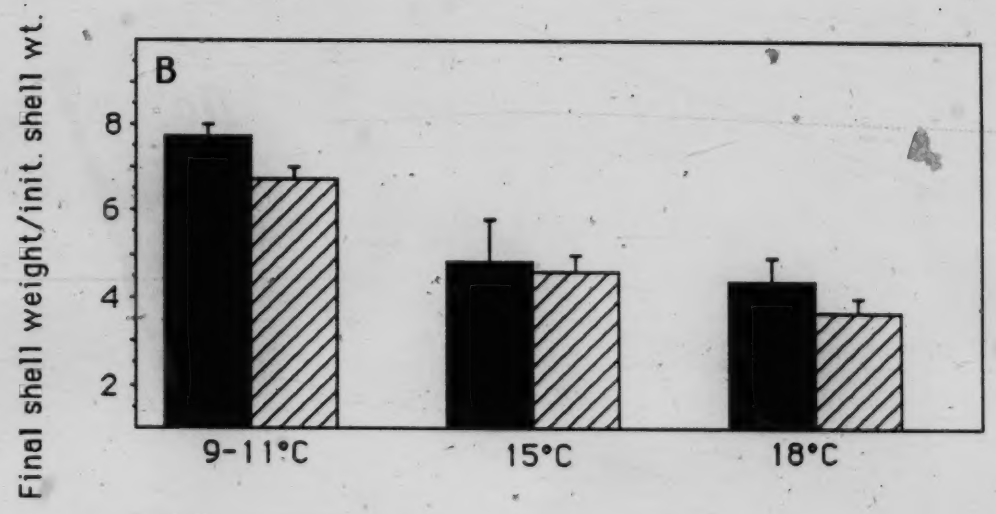

B
Final shell weight/init. shell wt.
8
6
4
2
9-11°C
15°C
18°C

Table II - 19. Tests for differences among water temperature treatments using results from two-way ANOVAs of spiral growth, and translation rate (shell length change/spiral growth) of *Thais lamellosa* juveniles raised in the absence of crabs, at a full food availability. The data are summarized in Table II-3, Figures II-16,17;A4-14. df = degrees of freedom, MS = mean square, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-values for the Site, Temperature, and Site-Temperature Interaction terms were calculated by dividing their respective MS values by the Replicate MS. The Replicate F-values were calculated by dividing the Replicate MS by the Error MS.

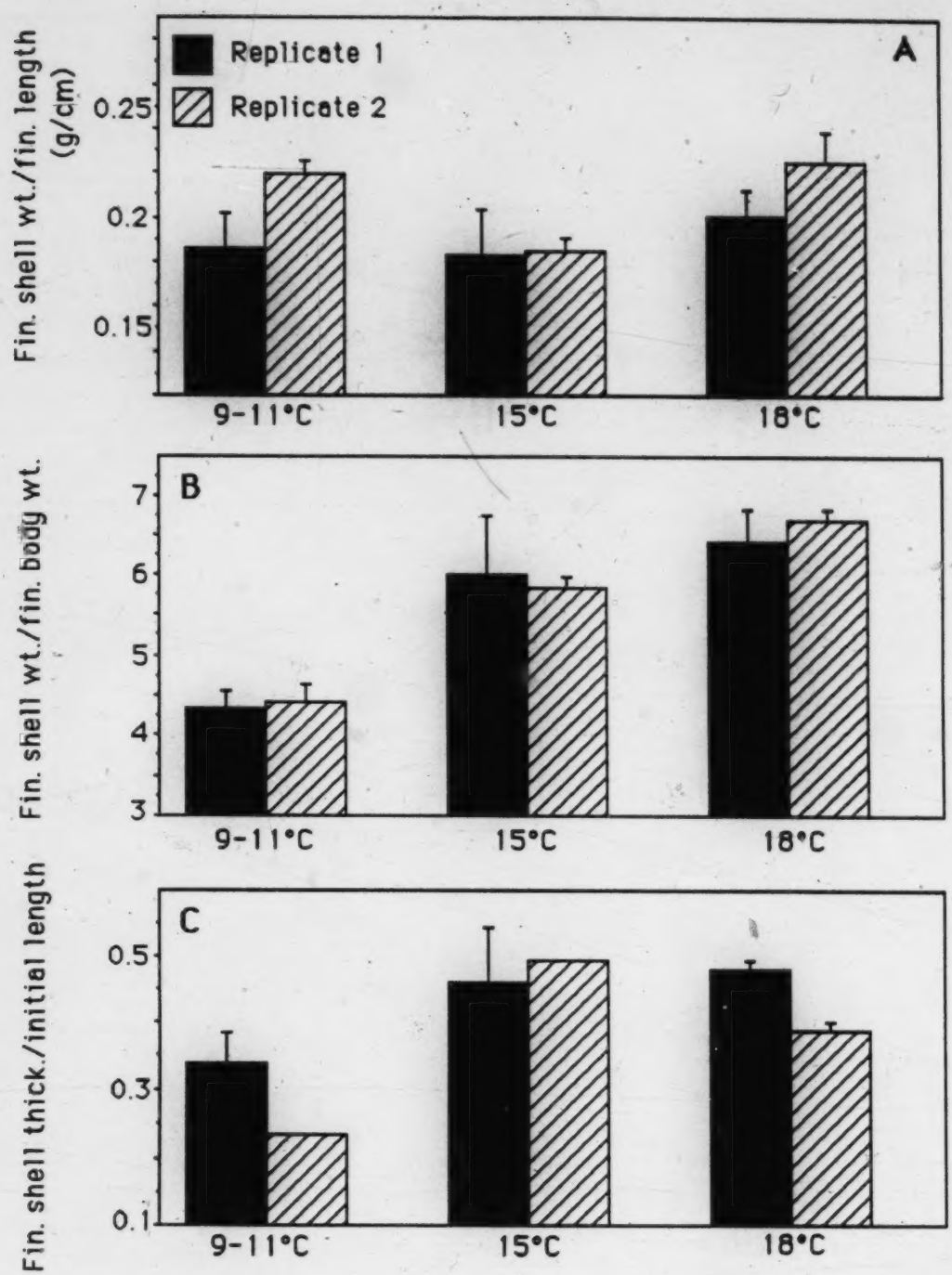
Factor	Spiral growth			Translation rate		
	df	MS	P	df	MS	P
Site	1	0.049	0.68	1	0.331	0.338
Temperature	2	5.972	0.002	2	3.030	0.000
Interaction	2	0.078	0.76	2	0.197	0.577
Replicate	6	0.269	0.331			
Error	104	0.231		107	0.357	

Table II-20. ANOVA tests for differences among water temperature treatments using ANOVA results of final shell thickness of *Thais lamellosa* juveniles raised in the absence of crabs, at a full food availability. The data are summarized in Table II-3, Figure A4-14.

Test	Factor	Final shell thickness/ Initial shell length		
		df	MS	P
Nested ANOVA of Argyle Creek snails only; and adjusted cell sizes	Temperature	2	0.091	0.03
	Replicate	3	0.007	0.66
	Error	6	0.012	
ANOVA of Replicate 1 snails only; and adjusted cell sizes	Site	1	0.042	0.12
	Temperature	2	0.111	0.01
	Interaction	2	0.020	0.29
	Error	6	0.015	

Figure II-17.

Differences in final shell morphology of snails from the water temperature experiment. All sites were pooled, and the means were calculated on the pooled data. The standard error bars in these diagrams represent the standard error between sites. (A = shell weight/shell length, B = shell weight/body weight, C = shell thickness/initial shell length.


Replicate 1
Replicate 2
A
Fin. shell wt./fin. length (g/cm)
0.25
0.2
0.15
9-11°C
15°C
18°C
B
Fin. shell wt./fin. body wt.
7
6
5
4
3
9-11°C
15°C
18°C
C
Fin. shell thick./initial length
0.5
0.3
0.1
9-11°C
15°C
18°C

significant differences in initial values (Table II-21). The scattergrams of these same data, however, revealed that these differences were again slight (Figure II-18). The ANCOVAs of final shell and body parameters, with initial shell weight as a covariate show a significantly lower amount of shell deposition with respect to body growth, but not to shell length, in snails raised at ambient temperatures, rather than at either 15° or 18°C (Table II-21). The scattergrams for these data further illustrate the relative variation in initial versus final measurements (Figures II-18,19). An explanation for the variation in the pre-experimental data could lie in the fact that due to the length of initial measurement time, the snails were exposed to the varied water temperatures and allowed to grow for a period of up to three days before being measured.

Discussion

Although all five sites differed in degree of both wave exposure and predation pressures from crabs, few site differences were found in response to the three types of experimental stimuli presented here, and the scattergrams of these data indicated these differences were slight. Such responses, although environmentally induced, must be strongly conserved to be maintained throughout populations which have not encountered stimuli such as crab predators for an indeterminate amount of time. The snails from each site did, however, maintain the colour and surface structures of their parent

Table II - 21. Tests for differences among water temperature treatments using adjusted means from ANCOVA analyses of the logged values of dry shell weight with respect to shell length and dry body weight in *Thais lamellosa* juveniles raised in the absence of crabs, with a full food availability. The data are summarized in Figures II-16,17,18. Y = adjusted mean, SE = standard error, P≤ 0.05 indicates a significant difference at a 95% confidence level in slopes or adjusted means. Initial shell weight was used as a second covariate for the final shell weight comparisons.

Axes	Site	Temperature						Common slope		Slope equality	Adjusted means
		Ambient(9-11°C)		15°C		18°C					
		Y	SE	Y	SE	Y	SE	Slope	SE	(P)	(P)
x = Log initial shell length (cm)	Argyle Crk.	-1.167	0.0069	-1.155	0.0080	-1.139	0.0640	2.617	0.0571	0.1420	0.0210
y = Log initial shell weight (g)	Mar Vista	-1.089	0.0084	-1.106	0.0098	-1.072	0.0084	2.768	0.0520	0.7540	0.0350
x = Log initial body weight (g)	Argyle Crk.	-1.157	0.0090	-1.168	0.0100	-1.140	0.0084	0.886	0.0250	0.4400	0.0900
y = Log initial shell weight (g)	Mar Vista	-1.070	0.0099	-1.091	0.0110	-1.084	0.0099	0.924	0.0200	0.1280	0.3500
x = Log final shell length (cm)	Argyle Crk.	-0.499	0.0200	-0.440	0.0170	-0.374	0.0180	2.040	0.1518	0.0810	0.0006
y = Log final shell weight (g)	Mar Vista	-0.544	0.0200	-0.435	0.0180	-0.348	0.0170	2.442	0.1435	0.7590	0.0000
x = Log final body weight (g)	Argyle Crk.	-0.472	0.0130	-0.442	0.0130	-0.409	0.0120	0.773	0.0373	0.3760	0.0110
y = Log final shell weight (g)	Mar Vista	-0.500	0.0140	-0.427	0.0140	-0.399	0.0120	0.717	0.0318	0.0030	0.0001

Figure II-18.

A.

Scattergrams of initial dry shell weight (g) versus initial shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

B.

Scattergrams of initial dry shell weight (g) versus initial dry body weight (g) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

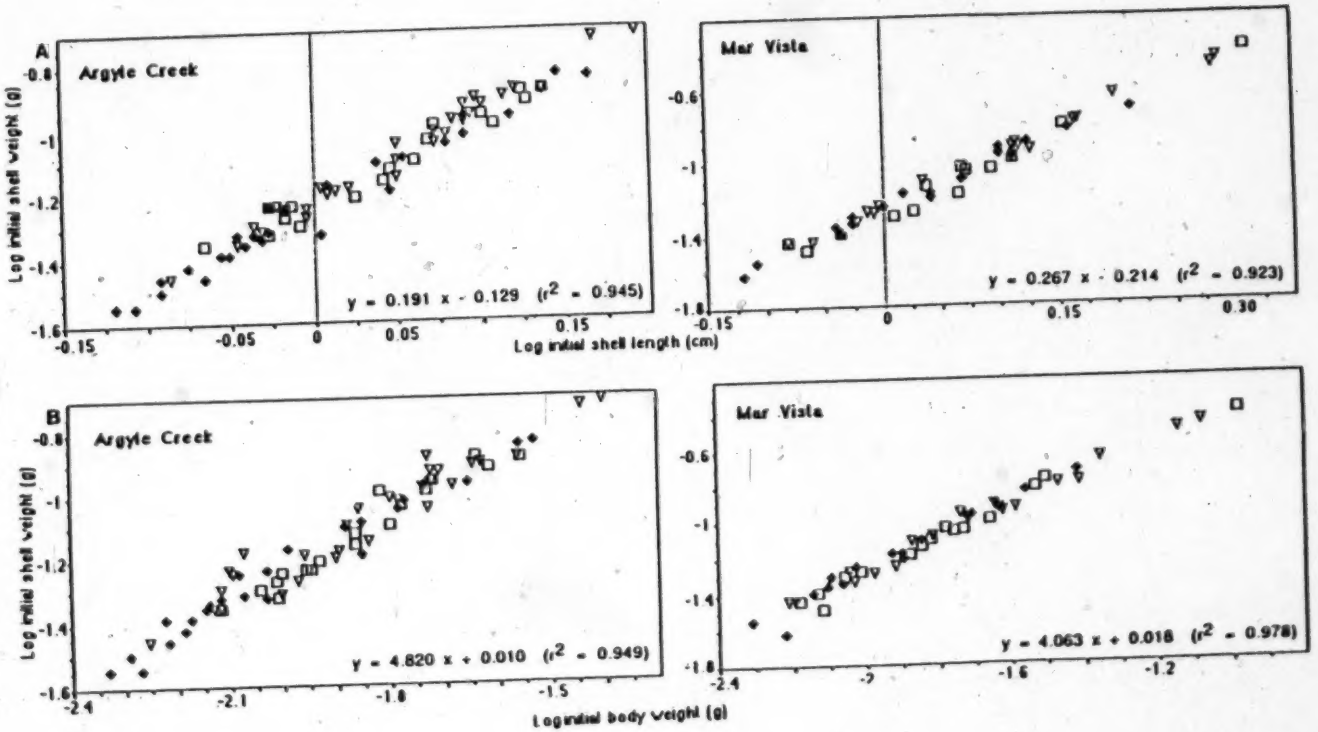

A
Argyle Creek
Log initial shell weight (g)
y = 0.191 x - 0.129 (r2 = 0.945)
Mar Vista
y = 0.267 x - 0.214 (r2 = 0.923)
Log initial shell length (cm)
B
Argyle Creek
Log initial shell weight (g)
y = 4.820 x + 0.010 (r2 = 0.949)
Mar Vista
y = 4.063 x + 0.018 (r2 = 0.978)
Log initial body weight (g)

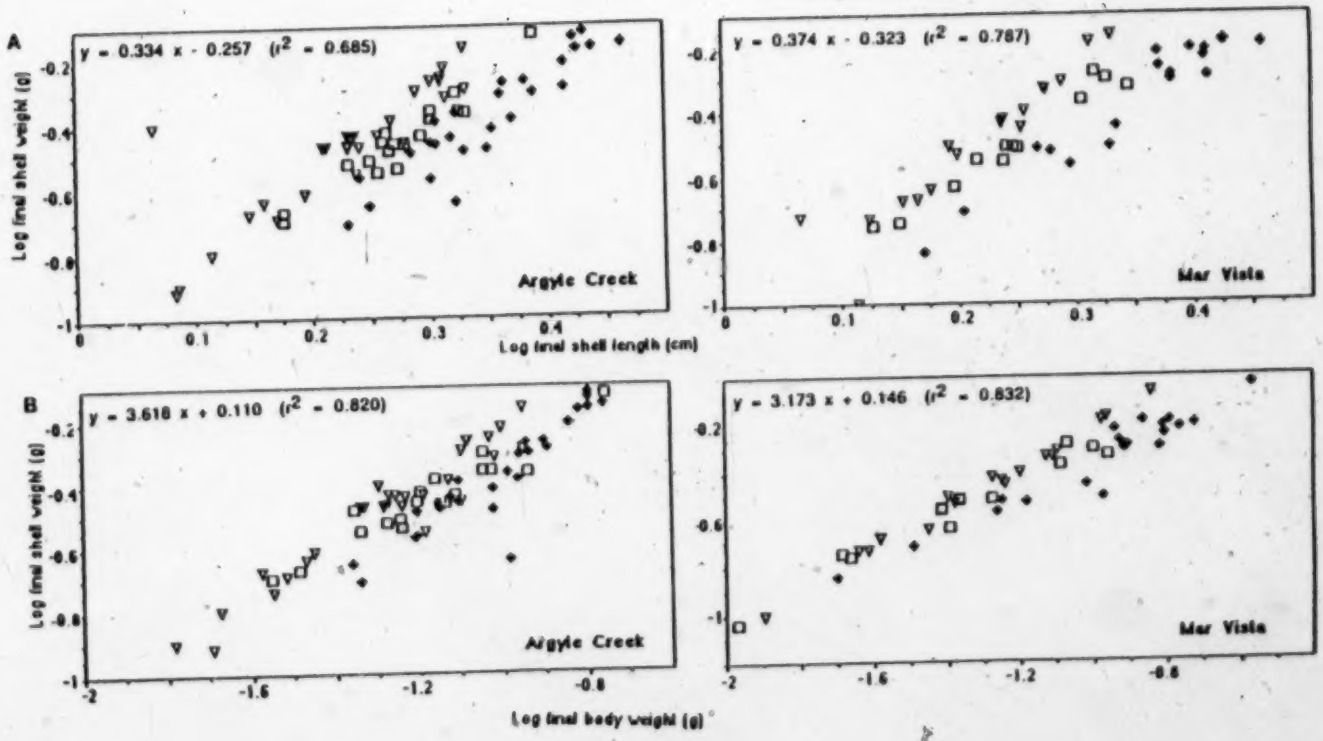
Figure II-19.

A.

Scattergrams of final dry shell weight (g) versus final shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), . □ = 15°C, . ▽ = 18°C.

B.

Scattergrams of final dry shell weight (g) versus final dry body weight (g) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.


A
y = 0.334 x - 0.257 (r^2 = 0.685)
Argyle Creek
y = 0.374 x - 0.323 (r^2 = 0.787)
Mar Vista
Log final shell weight (g)
Log final shell length (cm)
B
y = 3.618 x + 0.110 (r^2 = 0.820)
Argyle Creek
y = 3.173 x + 0.146 (r^2 = 0.832)
Mar Vista
Log final shell weight (g)
Log final body weight (g)

populations, despite the experimentally elicited responses (Figure II-20).

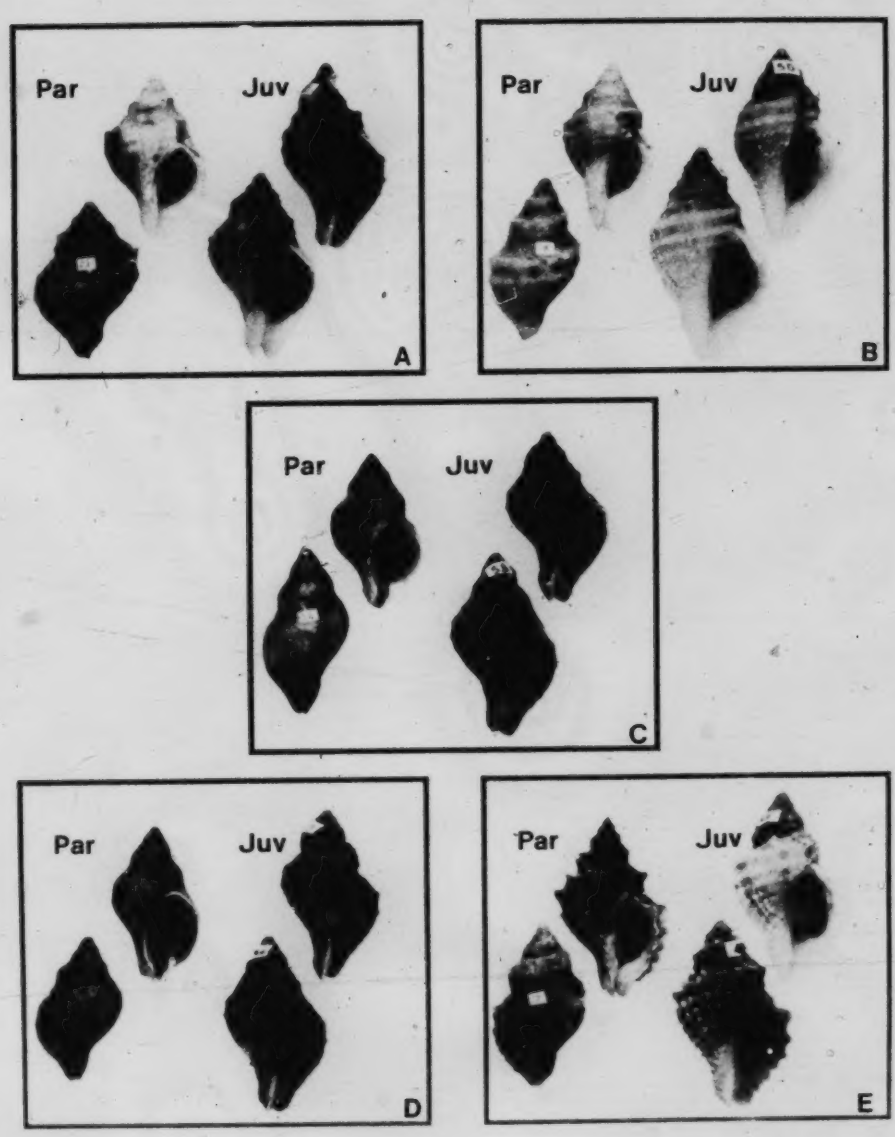
Site differences, however, were observed in apertural tooth development. Although snails from all sites exhibited some apertural tooth development when raised in the presence of crabs, snails from Argyle Creek were found to be significantly less prone to secrete apertural teeth than were snails from the remaining four sites (Table II-16). The natural populations of the collection site of Argyle Creek exhibited fewer sublethal crab predation scars than did snails of Aguilar Point, Cattle Point, and Mar Vista (Table II-1). No differences, however, were found in the response of snails from this former site with respect to final shell morphology (shell length, dry shell weight, dry body weight, spiral shell growth, and shell thickness) (ANOVA Table II- 11-13; means Table II-2).

A number of snails have been found to exhibit an avoidance behaviour in response to predators such as crabs (Vermeij,1978; Bertness *et al.*, 1981; Spight, 1983). This behaviour reduces time spent actively feeding (Bertness *et al.*, 1981; Spight, 1983). A number of morphological responses of snails to crabs, therefore, may be attributable to reduced feeding and slower growth rates. In these experiments growth rates varied repeatedly in response to crab scent and food availability. Some differences between treatments, however, were noted.

Snails raised with reduced food availabilities exhibited slower growth as measured by several parameters (shell length, shell weight, body weight, and spiral shell growth). In the presence of crabs, snails raised at a feeding rate of 100%, grew slower in all

Figure II-20.

A comparison of shell morphologies between adults from the parent populations and from laboratory raised juvenile *Thais lamellosa* from the same five populations. Par. = field collected adults, Juv. = laboratory raised juveniles, A-E = collection sites: A = Argyle Creek, B = Aguilar Point, C = Cattle Point, D = Mar Vista, E = Sanford Island. The average length was approximately 4 cm for the parent shells, and approximately 2 cm for the juvenile shells.


Par
Juv
A
Par
Juv
B
Par
Juv
C
Par
Juv
D
Par
Juv
E

parameters except shell weight. Snails raised both with limited and full food availabilities, and those raised in the presence of crabs, increased in shell apertural thickness. Little difference was found between snails raised with the 67% and the 100% food availabilities. Possibly the snails in both of these treatments were either i. approaching their maximal feeding rates, or ii. approaching their maximal growth rates. A large proportion of snails raised in the presence of crabs developed apertural teeth, while none of the juveniles of these experiments raised without crab influence showed any sign of apertural tooth development, although apertural tooth development is accepted to be related not only to the presence of crabs, but also to reduced feeding and slow growth rates (Appleton & Palmer, 1988). Possibly if lower levels of feeding had been used in the food availability experiment, not only may the food availability response have been exaggerated, but apertural tooth development may have been induced in snails raised in the absence of crabs. Food-limited individuals, however, did appear to require a lower stimulus to initiate apertural tooth development than did snails raised with full food available. With regard to other growth parameters, however, the response of snails raised with 33% food availability was less than those raised with 100% food.

Interestingly, with regard to a number of shell and body parameters, the snails of replicate two, raised in the presence of crabs, responded more strongly to the crab stimulus than did snails of replicate one. Such an increased response is probably due to the fact that the crabs of replicate two consumed almost twice the number of field-collected *Thais lamellosa* during the experimental

period than those of replicate one. This result indicates *Thais lamellosa* to have an inherent response to either the crab-produced metabolites, or to the scent of damaged conspecifics. The response of the snails to the crabs in this experiment, may in fact, not be due to the actual presence of the crab at all, but due to the scent of damaged conspecifics.

The secretion of a thicker shell with apertural teeth in the presence of crabs is an adaptive response. Crabs have been found to break snail shells through three basic methods: i. by crushing the shell, particularly across the body whorl, ii. by breaking the apex of the shell, and iii. by peeling or chipping at the aperture of the shell (Vermeij, 1987). The crab, *Cancer productus*, used in this experiment generally tends to attack at shell apertures (Zipser & Vermeij, 1978). Shell apertural thickening provides greater protection against such shell breaking forces (Vermeij, 1978; Bertness & Cunningham, 1981; Palmer, 1985). Furthermore, the function of apertural teeth has been suggested to be twofold: i. occlusion of the aperture, restricting insertion of chelae, and ii. provision of additional apertural thickening, and thus strengthening, at minimal cost of shell deposition (Appleton & Palmer, 1988).

Snails reared at increased water temperatures showed similar responses to those raised with limited food, including an increase in shell thickness combined with a reduction in growth of the remaining basic parameters. Tropical snails are known to secrete relatively thicker shells than their temperate counterparts (Vermeij, 1978). Because of the observed number of deaths, growth checks and abnormalities in the shells secreted by the experimental

animals maintained at increased temperatures (pers. obs.), it is apparent that higher temperatures produced a definite stress in these snails, and it appears unlikely that the secretion of thicker shells by these animals is comparable to those of natural tropical populations, but instead may simply be a response to reduced growth.

Shell thickening in response to reduced growth has been well documented (Vermeij, 1978; Spight, 1983; Wellington & Kuris, 1983). Such a response may reflect a fundamental type of predator avoidance: during periods of limited body growth, potential protection gained from increased shell thickness may outweigh the cost of actual shell deposition (Palmer, pers. comm.).

The morphological responses observed in these experiments represented responses to a change in the habitat, presumably for the worse, and involved an increased deposition of shell material or in shell thickness at the expense of growth in body weight and overall shell size. This additional secretion of shell material in "less-than-ideal" environmental conditions, further supports the supposition of long-term protection outweighing short-term growth.

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Chapter III.

Shell Microstructural Plasticity of *Thais lamellosa* in Response to Environmental Conditions

Introduction

Molluscan mineralogy and microstructure are both used extensively as taxonomic characters (Lindberg & Kellogg, 1982; Wellington & Kuris, 1983; Chen, 1985; Lindberg, 1986; Lindberg & Hickman, 1986). Also, several marked evolutionary trends have been described within molluscan shell microstructure. For example, primitive molluscs appear to have secreted primarily aragonite, while more advanced molluscs secrete either wholly calcitic shells or shells composed of a combination of calcite and aragonite (Taylor, 1973; Rhoads & Lutz, 1980). In addition, the outer prismatic layers are often lost evolutionarily (Taylor, 1973). Nacre is thought to be a primitive microstructure, as both pelecypods and gastropods exhibit a replacement of nacre with calcitic foliated or aragonitic crossed lamellar structure (Taylor, 1973; Rhoads & Lutz, 1980). This latter trend is not well understood and has been described as paradoxical (Taylor & Layman, 1972), although Palmer (1983) provides evidence suggesting a higher energetic cost of nacre secretion. Perhaps an examination of environmental effects on shell microstructure would lead to a better understanding of these trends.

Shell microstructural composition is known to be under environmental control to at least some degree (Rhoads & Lutz, 1980). Salinity, for example, is thought to be related to shell

calcite:aragonite ratios (Lowenstam, 1954a; Dodd, 1963). Bøggild (1930) found only one fresh water mollusc containing calcite in its shell. Eisma (1966), however, found no such relationship between salinity and shell mineralogy. Lowenstam (1954 a.b, 1964) found an inverse relationship between percent calcite versus aragonite in shells and temperature. In genera where individuals may secrete either a wholly calcitic or a mixed aragonitic-calcitic shell, it is the species containing calcite which are generally found to be natives of cooler, more temperate waters (Lowenstam, 1964). Taylor (1988) hypothesizes this latitudinal trend in shell mineralogy to be associated with the relative solubilities of both minerals at decreased temperatures. Dodd (1963, 1964) discovered several temperature-mineralogy trends in various *Mytilus* species. Individuals of *M. californianus* exceeding 15 mm in length were found to have a higher aragonite content if they initiated growth in the spring rather than in the fall. Dodd (1963) demonstrated a positive relationship between aragonite content and mean annual temperature of collection site in populations of *M. edulis*. Both seasonal and latitudinal variation was observed in the microstructural composition of the salt marsh mussel *Geukensia demissa* due to shell dissolution (Lutz and Clark, 1984). With the onset of autumn and cooler temperatures, dissolution in *G. demissa* begins in the inner nacreous layer. The nacre tablets tend towards irregularity, until, with continued dissolution, only a fine grained structure remains. Nacre is then re-secreted with the onset of spring. Lutz and Clarke (1984) also found that populations of *G. demissa* native to regions with higher mean water temperatures

have either a reduced occurrence of this fine grained structure or none at all, indicating that seasonal dissolution is reduced in warmer regions.

The actual deposition of shell material has an energetic cost. Some microstructural layers are thought to be more expensive to secrete than others (Vermeij & Currey, 1980; Palmer, 1983). One factor which may be directly proportional to this energetic cost is the amount of organic material present between the crystals (Palmer, 1983). The proportion of organic matrix varies among microstructures: nacre and simple prismatic structures, for example, have a significantly higher organic content than the remaining structures (Wainwright *et al*, 1976). The rate at which shell material can be deposited, and its consequent limitations on body growth rate, may be thought of as a non-energetic cost of shell secretion (Palmer, 1981). More organized microstructures such as crossed-lamellae are thought to be more time consuming to secrete than other, less organized structures (Vermeij & Currey, 1980). The extent to which food availability, rate of shell growth, and shell microstructural secretion are inter-related, however, is unknown. Prezant and Chalermwat (1983) found variations in the crossed-lamellar structure in the fresh water clam *Corbicula* to be associated with environmental factors, and its replacement with the less-ordered crossed acicular structure to be due to "less than ideal" trophic and temperature conditions.

Shell microstructural composition has been frequently associated with the life histories of organisms. Gabriel (1981) hypothesized that the inner nacreous-outer prismatic layer

composition of a number of molluscs reflected a compromise between an external protection against boring organisms and an internal layer of mechanically stronger material for protection against shell-breaking predators. The occurrence of both calcite and aragonite (Rhoads & Lutz, 1980) or of layers of alternating orientations of structures such as crossed lamellae (Currey & Kohn, 1976) are purported to hinder crack propagation. Burrowing pelecypods have been noted to secrete external layers of homogeneous, crossed lamellar, or prismatic structures, due, it is thought, to their superior ability to resist abrasion (Taylor & Layman, 1972; Gabriel, 1981). Vermeij and Currey (1980) noted a latitudinal trend in gastropod shell microstructural composition within the family Thaididae, with tropical species being composed entirely of crossed-lamellae, and temperate species of an "ill-defined crossed-lamellar" nature. Crushing strengths from this same study appear to indicate the tropical shells to be stronger. Vermeij and Currey (1980) postulate the observed variation in microstructure to be due to greater intensities of pressures by shell-breaking predators in tropical as opposed to temperate regions.

Although much of the control exerted over shell microstructure is of a genetic nature, the environment also plays a role (Rhoads & Lutz, 1980). The above studies do not enable separation of the effects of the genotype and the plasticity of the phenotype of the animals. These studies were also based on field collected animals, and little if any of their past growth history was known. Through a comparison of shell microstructures of laboratory-hatched snails,

raised under a variety of controlled environmental conditions, the plasticity of shell microstructural composition may be examined. Further, through the study of the responses of several genetically isolated populations, the genetic versus plastic components of shell microstructure may also be determined.

Methods

I. Collection sites and raising of hatchlings.

Adult individuals of *Thais lamellosa* were collected from five sites in the Pacific Northwest in September, 1986. These sites included Aguila Point (48°50'18"N, 125°18'24"W) and Sanford Island (48°52'18"N, 125°09'48"W), Barkley Sound, British Columbia, and Cattle Point (48°27'06"N, 122°57'42"W), Mar Vista (48°28'48"N, 123°04'W), and Argyle Creek (48°31'06"N, 123°00'48"W), San Juan Island, Washington. Proportional shell microstructural composition did not vary significantly between sites (Table III-1). Any between site variation, however, would most likely be masked by the high degree of within site variation. The snails used in this analysis were randomly collected at each site, and nothing is known of their past growth histories.

Adult snail and subsequent hatchling maintenance, as well as the experimental design, is described in Methods, Chapter II, Sections I and III.

Table III-1. Ratios of the thicknesses of crossed lamellar to prismatic layers in adult and juvenile *Thais lamellosa* shells from the five collection sites. SE = standard error, Max. = highest proportion, Min = lowest proportion, N = sample size

Site	Crossed lamellar/prismatic structures				
	Mean	SE	Min.	Max.	N
Argyle Crk.	0.205	0.022	0.134	0.351	23
Aguilar Pt.	0.148	0.028	0.037	0.359	26
Cattle Pt.	0.212	0.047	0.064	0.875	30
Mar Vista	0.132	0.010	0.057	0.207	29
Sanford Is.	0.120	0.015	0.056	0.222	28

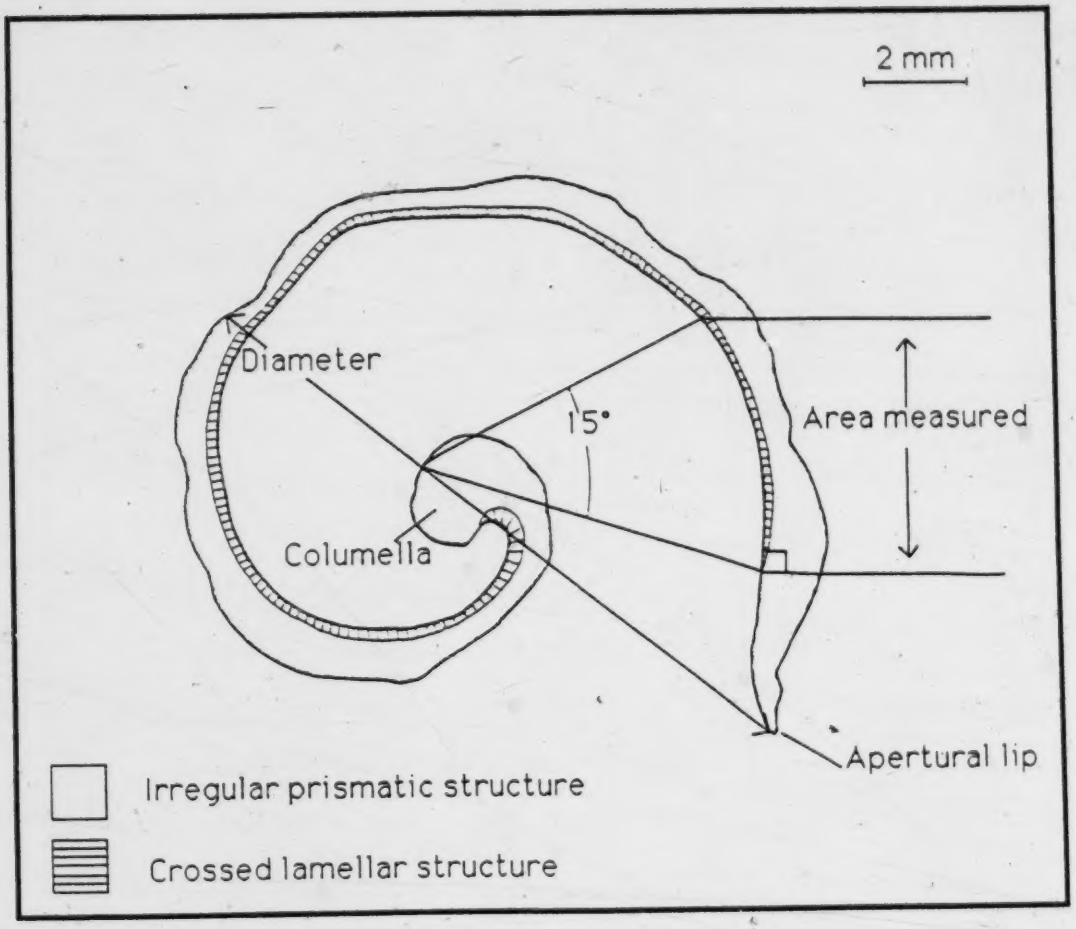
II. Measurements and analyses.

All experiments were conducted over a period of approximately three months, from the first of September to the end of November, 1987. At the end of the three month period, shell length (from the apex to the distal-most tip of the siphonal canal) was measured on each individual. At this point in time, all snails were terminated and their bodies removed from the shells. The shells were air dried for at least forty-eight hours prior to being cut with a diamond bit rock saw. The cut approximated the posterior-most spiral rib on the body whorl, perpendicular both to the growth lines and to the outer surface of the shell. The cut surface was polished with 600 grit, cleaned, air dried, and mounted onto a microscope slide with an epoxy resin (Epotek2 301). This mount was then placed into a drying oven and allowed to harden at 65°C for approximately twelve hours. The bulk of the excess shell was then cut away from the mount, again with a rock saw, leaving a stub of shell approximately 1.5 mm thick on the slide. The stub was ground down towards the slide and polished with 600 grit until the resulting section of shell was sufficiently thin for the transmission of light (see Figure III-1 for a representative section).

Camera lucida sketches were drawn from the magnified thin sections. The areas of both the inner cross lamellar and the outer prismatic microstructural layers over a calculated distance were measured from the camera lucida sketches. A stationary endpoint of the area to be measured was set at the point of last secretion of crossed lamellae. Shell diameter (across the body whorl, cutting through both the apertural lip and the indentation of the shell just

Figure III-1.

Diagram of a thin section of a juvenile *Thais lamellosa* shell, through the posterior-most rib of the body whorl. The section was cut approximately perpendicular to both the surface growth lines and to the outer surface of the shell.


2 mm
Diameter
15°
Area measured
Columella
Apertural lip
Irregular prismatic structure
Crossed lamellar structure

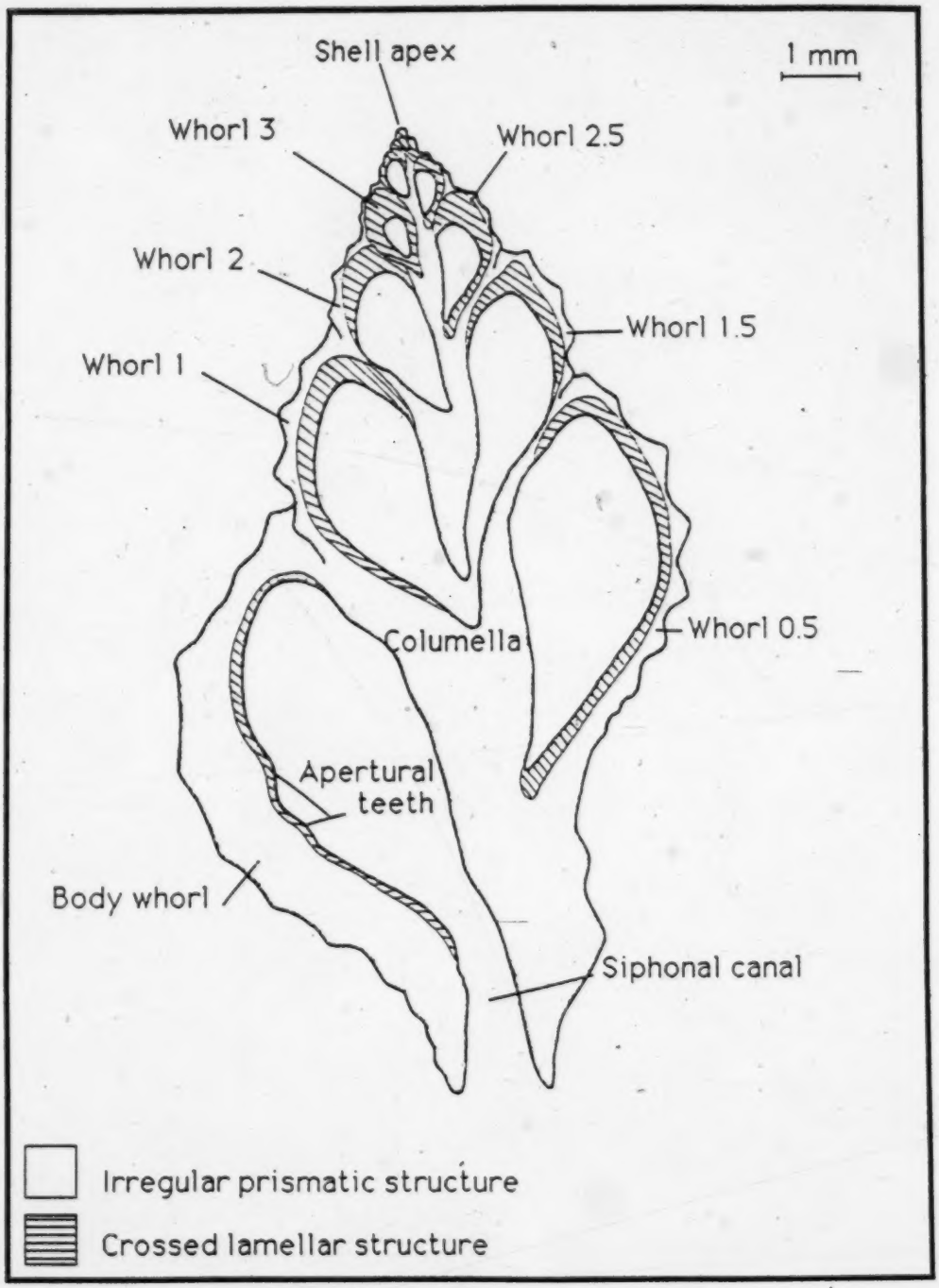
prior to the columella) was estimated by approximating the section to be a circle. The second endpoint of the area to be measured was determined by calculating an arc length for an angle of 15° and extending this length from the fixed, first endpoint towards the columella, away from the apertural lip (Figure III-1). Such a method allowed for standardization for shell size. The areas of both layers were determined through the use of a MacIntosh 512 Summographics tablet, the MacIntosh MacMeasure program, and the camera lucida sketches. Layer thicknesses were estimated by dividing the layer areas by the distance over which it was measured.

Longitudinal sections were cut on randomly selected experimental juvenile *Thais lamellosa*. The sections ran through both the shell apex and the siphonal canal, at approximately right angles to the apertural lip. Measurements of microstructural layer thicknesses were taken immediately anterior to the posterior-most spiral rib on each half whorl of the section (see Figure III-2 for a diagrammatic view). The use of juvenile snails with intact protoconchs, as well as taking the measurement just anterior to the posterior-most spiral rib on each whorl made it unnecessary to take erosive forces into account. For comparative purposes, longitudinal sections were also cut on adult, field collected individuals.

Individual layer thicknesses and the proportion of crossed lamellar layer thickness to total shell length were compared through analyses of variance (ANOVA) as described for shell thickness in Methods, Chapter II.

Figure III- 2.

Diagram of a longitudinal thin section through the shell of a juvenile *Thais lamellosa*. The section approximately bisects the shell, parallel to both the surface growth lines and to the apertural lip. Note the increasing proportion or crossed lamellae to simple prisms towards the shell apex.


Shell apex
1 mm
Whorl 3
Whorl 2.5
Whorl 2
Whorl 1.5
Whorl 1
Columella
Whorl 0.5
Apertural teeth
Body whorl
Siphonal canal
Irregular prismatic structure
Crossed lamellar structure

All basic statistics, t-tests, and ANOVAs were conducted using the Statview 512+™ (Abacas Concepts, Berkley, Ca.) microcomputer statistical package.

Results

Food availability.

The ANOVA results (Table III-4; means Table III-2) of shell microstructural layer comparisons reveal a significant increase in the thickness of both the crossed lamellar and the prismatic layers in snails raised with 33% food availability over snails raised with either 67 or 100% food (Figures III-3, A5-1,2,3). Little difference was found between these latter two food categories. The proportion of crossed lamellae to total shell thickness, however, did not vary among food treatments. These data also suggest site differences in both of the layer thicknesses, but site differences were not consistent between replicates, nor with the estimated level of predation pressure at each site. The site-food interaction term was not significant.

Crab presence.

Data (ANOVA Table III-5; means Table III-2; Figures III-4, A5-4,5,6) from snails raised at both 33 and 100% food availabilities indicate no significant difference between treatments in the thickness of the crossed lamellar layer, but show a marked increase in thickness in the prismatic layer of snails maintained in the presence of crabs. The proportion of crossed lamellae to total shell

Table III - 2. Means and standard errors of shell microstructural layer thicknesses for juvenile *Thais lamellosa* raised in the laboratory at ambient water temperature (9-11°C), in the presence and absence of crabs, and at three food availabilities. SE = standard error, N = sample size

Food avail.	Crabs	Replicate	Study site	Thickness crossed lamellae (mm)		Thickness simple prisms (mm)		C. lamellar/ total thickness		N
				Mean	SE	Mean	SE	Mean	SE	
Fed 33 %	No crabs	1	Argyle Crk.	-	-	-	-	-	-	0
			Aguilar Pt.	-	-	-	-	-	-	0
			Cattle Pt.	-	-	-	-	-	-	0
			Mar Vista	0.0502	0.044	0.5421	0.553	0.087	0.007	7
			Sanford Is.	0.0451	0.075	0.6678	1.331	0.074	0.021	5
		2	Argyle Crk.	0.0418	0.026	0.6701	0.827	0.062	0.008	5
			Aguilar Pt.	0.0698	0.098	0.9956	2.603	0.073	0.020	3
			Cattle Pt.	0.0477	0.029	0.7346	0.558	0.063	0.006	8
			Mar Vista	0.0450	0.026	0.7063	0.491	0.060	0.001	3
			Sanford Is.	0.0419	0.031	0.5674	0.815	0.071	0.004	4
Fed 33 %	Crabs	1	Argyle Crk.	-	-	-	-	-	-	0
			Aguilar Pt.	-	-	-	-	-	-	0
			Cattle Pt.	0.0249	-	0.8109	-	0.030	-	1
			Mar Vista	0.0553	0.046	1.0830	4.000	0.057	0.024	2
			Sanford Is.	0.0488	0.113	1.0290	3.194	0.047	0.007	3
		2	Argyle Crk.	0.0508	0.067	1.2600	1.648	0.042	0.009	5
			Aguilar Pt.	-	-	-	-	-	-	0
			Cattle Pt.	0.0438	0.036	1.3240	0.901	0.032	0.002	8
			Mar Vista	-	-	-	-	-	-	0
			Sanford Is.	0.0623	0.112	2.0850	0.083	0.029	0.005	2
Fed 67 %	No crabs	1	Argyle Crk.	0.0353	0.046	0.4303	0.466	0.079	0.008	8
			Aguilar Pt.	0.0413	0.041	0.5953	1.738	0.073	0.016	3
			Cattle Pt.	0.0367	0.029	0.4107	0.351	0.085	0.009	8
			Mar Vista	0.0360	0.021	0.4364	0.466	0.081	0.007	10
			Sanford Is.	0.0376	0.039	0.4470	1.042	0.088	0.027	3
		2	Argyle Crk.	0.0438	0.051	0.5130	0.454	0.079	0.008	7
			Aguilar Pt.	0.0344	0.027	0.5819	0.543	0.060	0.009	7
			Cattle Pt.	0.0367	0.033	0.5548	0.603	0.065	0.008	6
			Mar Vista	0.0349	0.061	0.4063	0.386	0.081	0.015	5
			Sanford Is.	0.0333	0.045	0.3550	0.252	0.087	0.011	7
Fed 100 %	No crabs	1	Argyle Crk.	0.0480	0.052	0.6358	0.545	0.071	0.008	7
			Aguilar Pt.	0.0539	0.050	0.6936	0.675	0.073	0.005	5
			Cattle Pt.	0.0382	0.048	0.5510	0.254	0.066	0.009	6
			Mar Vista	0.0280	0.039	0.7054	2.058	0.043	0.011	3
			Sanford Is.	0.0368	0.039	0.5170	1.334	0.076	0.016	4
		2	Argyle Crk.	0.0390	0.056	0.5084	0.670	0.072	0.006	5
			Aguilar Pt.	0.0462	0.036	0.6342	0.456	0.068	0.005	6
			Cattle Pt.	0.0444	0.057	0.4511	0.750	0.096	0.014	7
			Mar Vista	0.0428	0.056	0.6310	1.118	0.073	0.012	7
			Sanford Is.	0.0551	0.064	0.5988	0.650	0.088	0.016	4
Fed 100 %	Crabs	1	Argyle Crk.	0.0483	0.072	1.1240	2.310	0.047	0.012	4
			Aguilar Pt.	0.0410	0.063	1.0740	0.863	0.037	0.005	6
			Cattle Pt.	0.0333	0.032	0.7534	0.695	0.044	0.005	9
			Mar Vista	0.0327	0.110	0.5032	0.595	0.059	0.013	2
			Sanford Is.	0.0517	0.053	0.7364	0.862	0.067	0.007	4
		2	Argyle Crk.	0.0418	0.049	1.1120	1.585	0.038	0.005	7
			Aguilar Pt.	0.0444	0.061	1.3800	1.263	0.034	0.006	9
			Cattle Pt.	0.0432	0.069	1.3770	2.435	0.031	0.004	4
			Mar Vista	0.0529	0.055	1.1950	1.699	0.047	0.007	8
			Sanford Is.	0.0471	0.052	1.2380	0.942	0.038	0.005	9

Table III - 3. Means and standard errors of shell microstructural layer thicknesses for juvenile *Thais lamellosa* raised in the laboratory in the absence of crabs, at 100% food availability, and at three water temperatures. SE = standard error, N = sample size

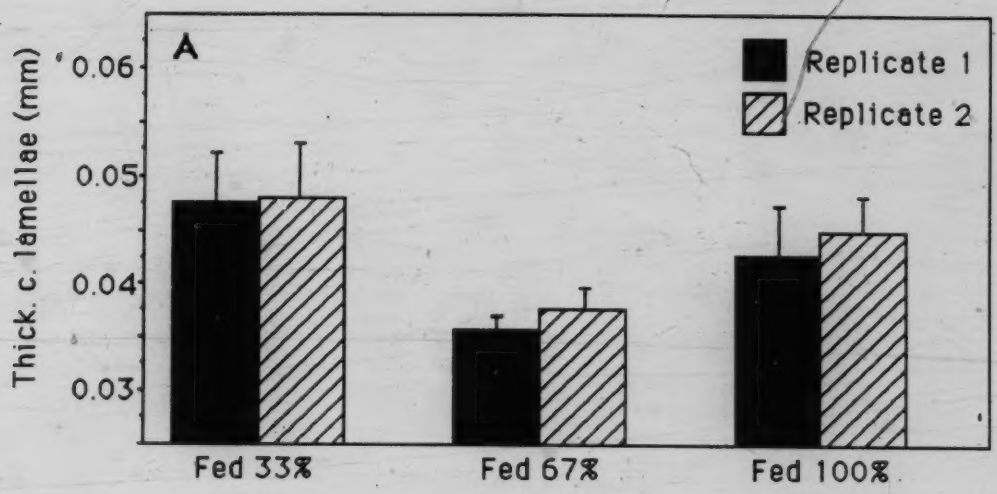
Temperature (Celcius)	Replicate	Study site	Thickness crossed lamellae (mm)		Thickness simple prisms (mm)		C. lamellar / total thickness		N
			Mean	SE	Mean	SE	Mean	SE	
Ambient (9-11°C)	1	Argyle Crk.	0.0692	0.073	0.1570	0.332	0.314	0.068	2
		Mar Vista	0.0856	0.058	0.1752	0.060	0.328	0.020	4
	2	Argyle Crk.	0.0571	0.013	0.1412	0.048	0.288	0.012	2
		Mar Vista	-	-	-	-	-	-	0
15°C	1	Argyle Crk.	0.1066	0.073	0.1709	0.045	0.383	0.014	5
		Mar Vista	0.1024	0.028	0.1800	0.378	0.390	0.064	4
	2	Argyle Crk.	0.0854	0.083	0.1865	0.083	0.313	0.019	3
		Mar Vista	0.0936	-	0.1419	-	0.398	-	1
18°C	1	Argyle Crk.	0.0923	0.072	0.1818	0.201	0.343	0.041	4
		Mar Vista	0.0976	0.076	0.1988	0.132	0.330	0.023	4
	2	Argyle Crk.	0.0807	0.150	0.1897	0.095	0.296	0.049	3
		Mar Vista	0.0877	-	0.1911	-	0.315	-	1

Table III - 4: Tests for differences among food availability treatments using results from two-way ANOVAs of shell microstructural layer thicknesses of *Thais lamellosa* juveniles raised in the absence of crabs, at ambient water temperature (9-11°C). The data are summarized in Table III-2, Figures III-3; A5-1,2,3. df = degrees of freedom, MS = mean square, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-value for the site term was calculated by dividing its MS by the MS of the site-replicate term. Similarly, the food MS and the site-food interction MS were divided by the MS for the food-replicate interaction and the site-food-replicate interaction MS, respectively. The remaining MS terms were divided by the error MS to calculate their F-values.

Factor	df	Crossed lamellar structure		Prismatic structure		Crossed lamellar/ total thickness	
		MS	P	MS	P	MS	P
Site	4	0.035	0.0750	0.070	0.0050	0.007	0.8600
Food availability	2	0.199	0.0001	0.352	0.0001	0.018	0.4500
Interaction	8	0.019	0.3300	0.017	0.4720	0.029	0.2700
Error	136	0.016		0.018		0.023	

Figure III-3.

Relative final shell microstructural layer thicknesses of snails from the food availability experiment. All sites were pooled, and the means were calculated on the pooled data. The standard error bars in these diagrams represent the standard error among sites. Prismatic layer thickness was similar in among treatment pattern to crossed lamellar thickness.
A = crossed lamellar thickness, B = crossed lamellar thickness/total shell thickness.


A
Replicate 1
Replicate 2
Thick. c. lamellae (mm)
0.06
0.05
0.04
0.03
Fed 33%
Fed 67%
Fed 100%

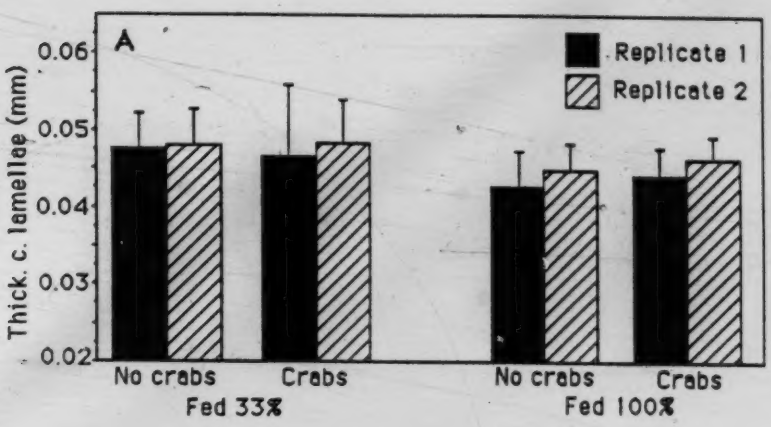
B
Thick. c. lam./total thick.
0.1
0.08
0.06
0.04
Fed 33%
Fed 67%
Fed 100%

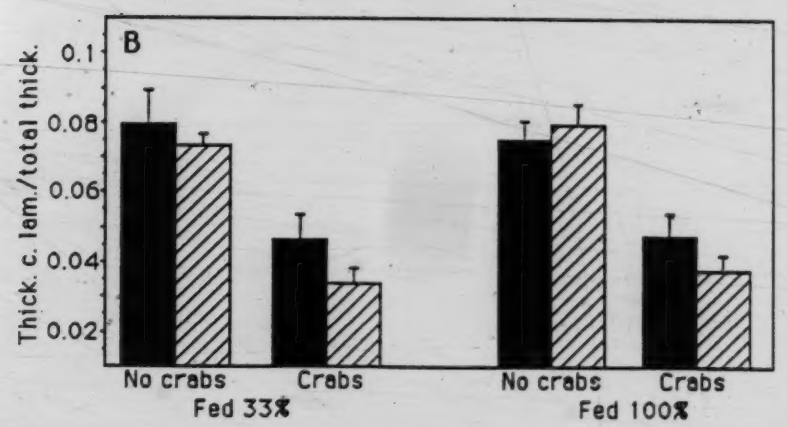
Table III - 5: Tests for differences between crab exposure treatments using results from two-way ANOVAs of shell microstructural layer thicknesses of *Thais lamellosa* juveniles raised at ambient water temperature (9-11°C), at two food availabilities. The data are summarized in Table III-2, Figures A5-4,5,6.df = degrees of freedom, MS = mean squares, P≤ 0.05 indicates a significant difference at a 95% confidence level in shell or body parameters. The F-values for the Site, Crab, and Site-Crab Interaction terms were calculated by dividing their respective MS values by the Replicate MS. The Replicate F- value was calculated by dividing the Replicate MS by the Error MS.

Food avail.	Factor	df	Crossed lamellar structure		Prismatic structure		Crossed lamellar/ total thickness	
			MS	P	MS	P	MS	P
Fed 33%	Crab	1	0.003	0.73	0.345	0.13	0.271	0.14
	Replicate	2	0.023	0.38	0.054	0.09	0.046	0.21
	Error	13	0.022		0.019		0.026	
Fed 100%	Site	4	0.021	0.57	0.016	0.90	0.023	0.67
	Crab	1	0.006	0.64	0.881	0.004	0.660	0.002
	Interaction	4	0.008	0.87	0.034	0.70	0.048	0.35
	Replicate	10	0.028	0.09	0.061	0.01	0.039	0.12
	Error	39	0.015		0.020		0.023	

Figure III-4.

Differences in final shell microstructural layer thicknesses of snails from the crab-exposure experiment. All sites were pooled and the means were calculated on the pooled data. The standard error bars of these diagrams represent the standard error among sites. A = crossed lamellar thickness, B = crossed lamellar thickness/total shell thickness.


A
Replicate 1
Replicate 2
Thick. c. lamellae (mm)
0.06
0.05
0.04
0.03
0.02
No crabs
Crabs
No crabs
Crabs
Fed 33%
Fed 100%


B
Thick. c. lam./total thick.
0.1
0.08
0.06
0.04
0.02
No crabs
Crabs
No crabs
Crabs
Fed 33%
Fed 100%

thickness is significantly lower in crab-influenced snails raised at 100% food, but is significantly lower only at a 90% confidence level in snails from the 33% food category.

Apertural teeth composed almost entirely of prisms were found in a number of snails raised in the crab-presence treatment, although teeth of field collected adults were found to be of crossed lamellae (Figure III-3). None of the snails maintained in the absence of crab influence exhibited a tendency towards the secretion of apertural teeth.

Temperature.

Thicknesses of both the crossed lamellar and prismatic layers increased in snails raised at elevated water temperatures (15° and 18°C) over snails maintained at ambient temperatures (9-1°C) (Table III-6, Figures III-6, A5-7). The proportion of crossed lamellar structure to total shell thickness, however, did not vary. Neither the site, nor the site-interaction terms were significant.

Longitudinal sections.

Longitudinal sections through the shell (siphonal canal and apex) revealed increasing proportions of crossed lamellar to prismatic structure tending towards the shell apex (Figures III-2, III-8).

In field collected adults, the crossed lamellar structure may be of two orientations: radial and concentric. The number of orientations increased towards the shell apex (Figure III-7). Because no clear demarcation was found between these orientations, they were assumed to be sublayers.

Figure III-5.

Diagrams of thin sections through the posterior-most rib of the body whorl of *Thais lamellosa* shells. Each of the sections was cut approximately perpendicular to both the surface growth lines of the shell, and to the outer surface of the apertural lip.

A.

Thin section of a juvenile *Thais lamellosa* raised in the laboratory in the presence of crabs. Note the formation of apertural teeth composed almost entirely of prisms.

B.

Thin section of an adult *Thais lamellosa* collected as an adult from a site with little or no large crab predators. Note the formation of apertural teeth composed entirely of crossed lamellae.

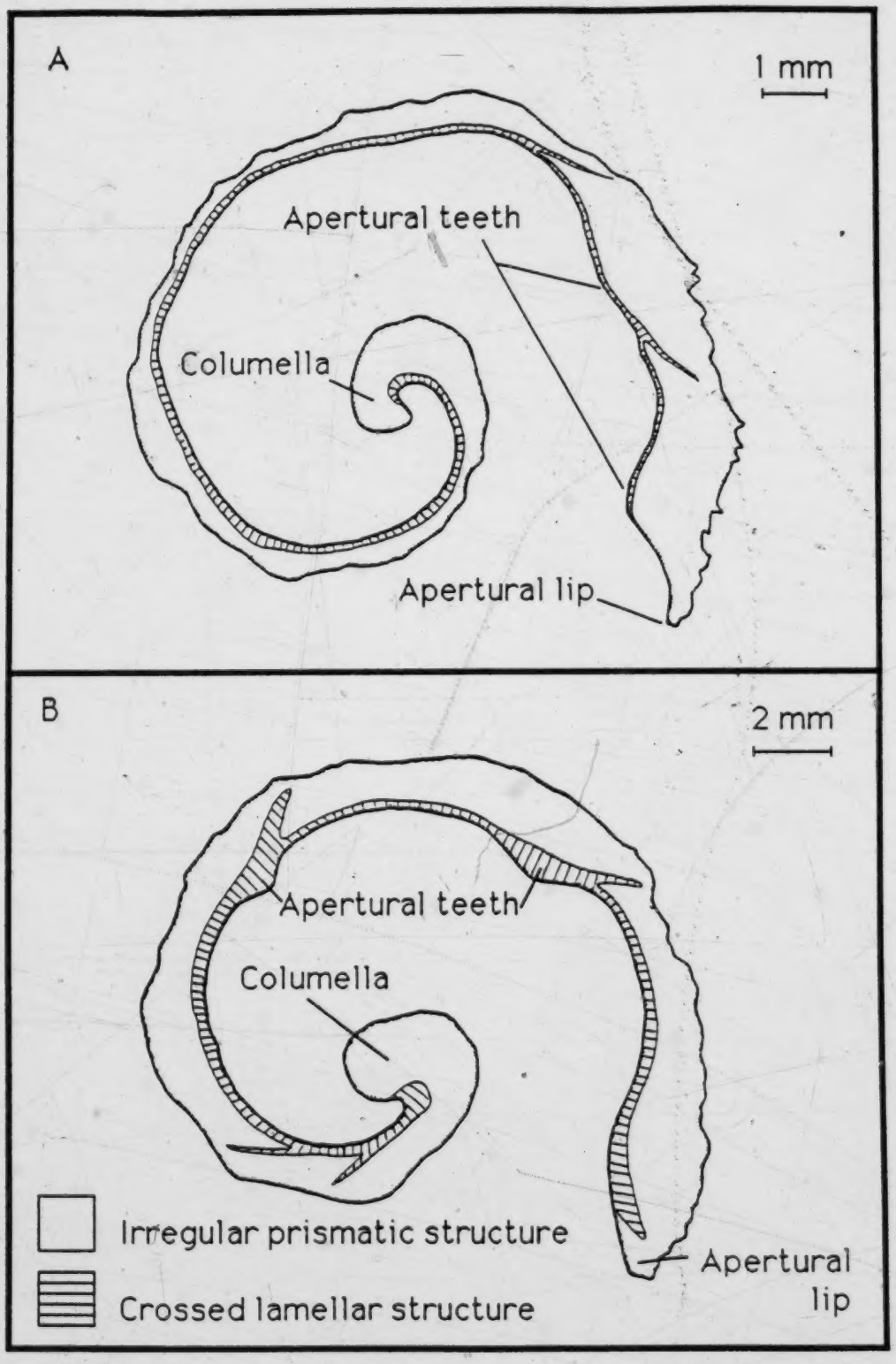

A
1 mm
Apertural teeth
Columella
Apertural lip
B
2 mm
Apertural teeth
Columella
Irregular prismatic structure
Crossed lamellar structure
Apertural lip

Table III - 6: Tests for differences among water temperature treatments using ANOVA results of shell microstructural layer thicknesses of *Thais lamellosa* juveniles raised in the absence of crabs, and with100% food. The data are summarized in Table III-3, Figures III-6; A5-7. Due to a missing cell, only snails from Argyle Creek are represented.

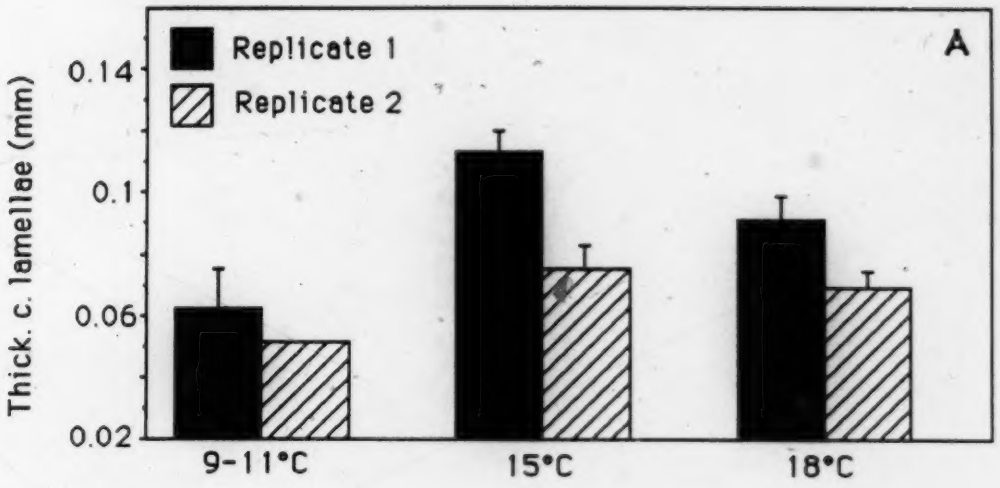
Factor	df	Crossed lamellar structure		Prismatic structure		Crossed lamellar/ total thickness	
		MS	P	MS	P	MS	P
Temperature	2	0.111	0.35	0.095	0.04	0.038	0.59
Replicate	3	0.073	0.08	0.008	0.76	0.061	0.34
Error	6	0.020		0.019		0.045	

Table III-7. Tests for differences among water temperature treatments using ANOVA results of shell microstructural layer thicknesses of Thais lamellosa juveniles raised in the absence of crabs, and with 100% food. The data are summarized in Table III-3, Figures III- 4; A5-7. Due to a missing cell, only snails from Replicate 1 are represented.

Factor		Crossed lamellar structure		Prismatic structure		Crossed lamellar/ total thickness	
	df	MS	P	MS	P	MS	P
Site	1	0.009	0.53	0.025		0.016	0.52
Temperature	2	0.111	0.04	0.069		0.039	0.38
Interaction	2	0.014	0.518	0.003	0.82	0.008	0.80
Error	6	0.019		0.016		0.034	

Figure III-6.

Differences in final shell microstructural layer thicknesses of snails from the water temperature experiment. All sites were pooled, and the means were calculated on the pooled data. The standard error bars of these diagrams represent the standard error between sites. Prismatic layer thicknesses were similar in among treatment pattern to crossed lamellar thickness. A = crossed lamellar thickness, B = crossed lamellar thickness/total shell thickness.


Replicate 1
Replicate 2
A
Thick. c. lamellae (mm)
0.14
0.1
0.06
0.02
9-11°C
15°C
18°C

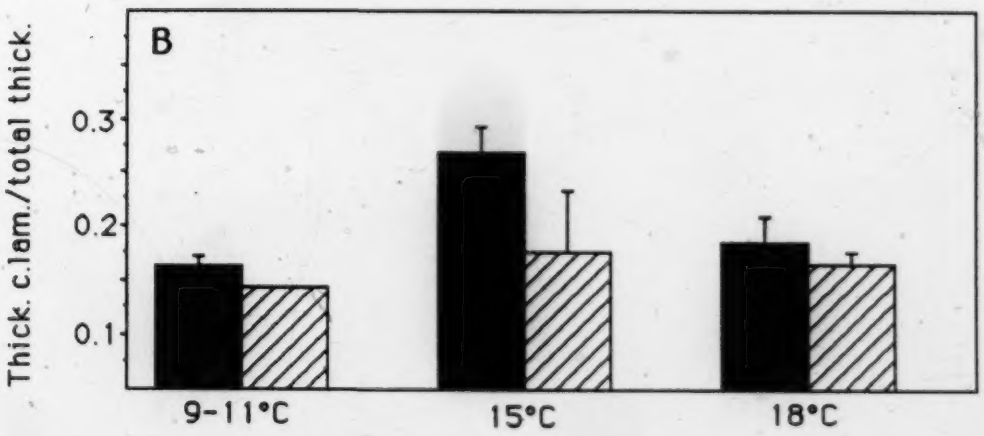

B
Thick. c.lam./total thick.
0.3
0.2
0.1
9-11°C
15°C
18°C

Figure III-7.

Representative diagram of a longitudinal thin section through the shell of an adult *Thais lamellosa*. The section approximately bisects the shell, parallel to both the surface growth lines of the shell and to the apertural lip. Note the increased number of orientations of crossed lamellar structure towards the shell apex.

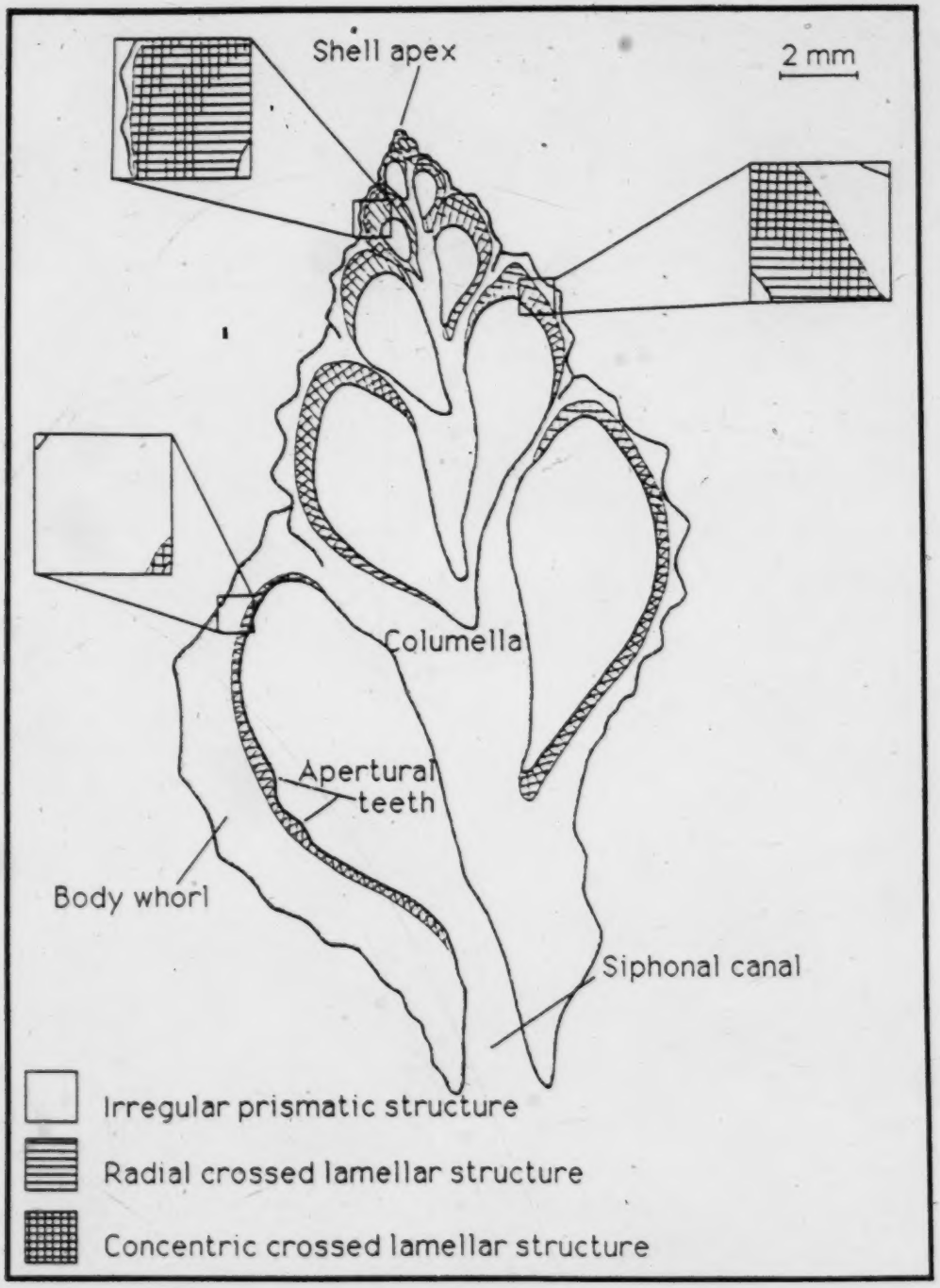
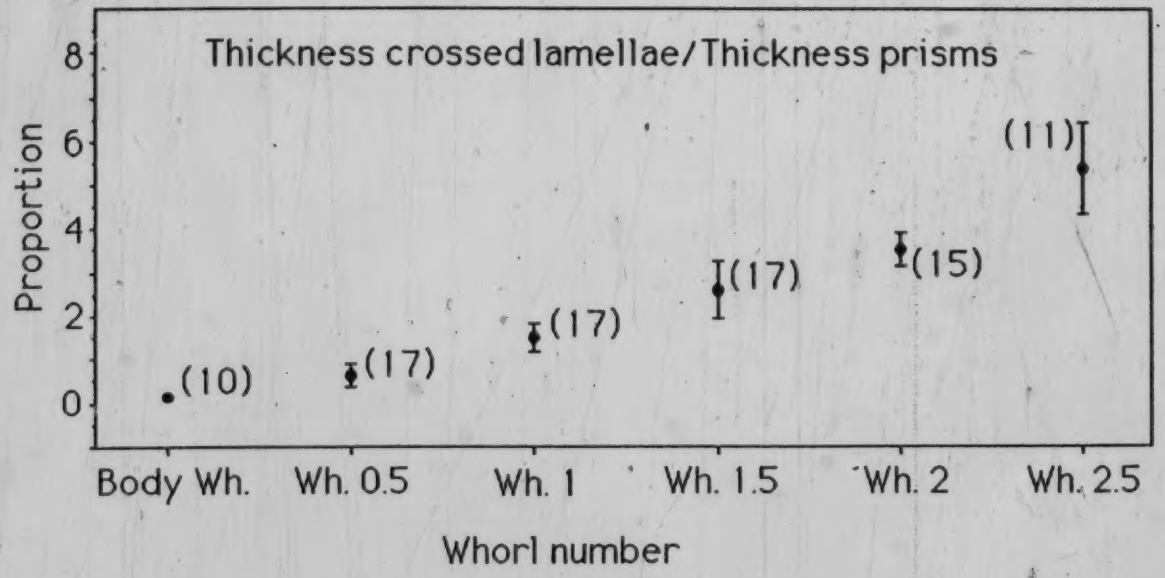

Shell apex
2 mm
Columella
Apertural teeth
Body whorl
Siphonal canal
Irregular prismatic structure
Radial crossed lamellar structure
Concentric crossed lamellar structure

Figure III-8.

Proportion of the relative thicknesses of crossed lamellar to prismatic structures with respect to whorl number. Measurements were taken every half whorl, and the whorls numbered accordingly, beginning with the body whorl, and extending towards the apex of the shell. The means, standard error bars, and sample size () are shown in the diagram. Experimental *Thais lamellosa* juveniles from all sites and all food availability and crab exposure treatments are represented.


Thickness crossed lamellae/Thickness prisms
Proportion
8
6
4
2
0
(10)
(17)
(17)
(17)
(15)
(11)
Body Wh.
Wh. 0.5
Wh. 1
Wh. 1.5
Wh. 2
Wh. 2.5
Whorl number

Discussion

Prismatic microstructures which are relatively high in organic material are more energetically expensive to produce than structures low in organics, such as crossed lamellae (Palmer, 1983). Snails from the food availability experiment, although varying markedly between treatments in both layer thicknesses, maintained similar proportions of both shell microstructures (ANOVA Table III-4; means Table III-2). Several explanations for this constancy are possible: i. the food availability treatments used in this experiment did not restrict food consumption sufficiently to produce a measurable response, ii. shell secretion is physiologically limited by some factor other than energetics, and iii. the maintenance of such uniform proportions of microstructural layers is of sufficient importance for food consumption and secretional costs to be negligible. A reduction of food available (33%) produced a definite decline in snail growth (see Chapter II), hence this food restriction should have been sufficient to produce a shell microstructural response.

Tropical meso- and neogastropods generally secrete shells entirely composed of aragonitic crossed lamellae. This latter trend has been attributed to i. increased water temperatures and the relative solubilities of calcite and aragonite (Taylor, 1988) or ii. to increased predation pressures in tropical versus temperate regions (Vermeij & Currey, 1980). In the experiments described here, snails raised at three water temperatures, although varying

greatly in growth patterns between treatments (see Chapter II), maintained relatively constant proportions of the two microstructural layers (ANOVA Table III-6; Figure III-6).

Although the proportional deposition of both microstructural layers remained constant between the water temperature treatments, these proportions differed markedly from those of the food availability experiment (means Tables III-2,3). Snails maintained in the recirculating systems of the water temperature experiment secreted a proportionally greater amount of crossed lamellae (means Table III-3) than those of the food availability experiment in which the sea water was constantly flowing. Water was replaced once every two weeks in the recirculating systems, but this microstructural variation between experiments indicates that some element, directly or indirectly associated with shell production, was limited to these snails. The state of health of the snails raised at elevated water temperatures was somewhat questionable (see Discussion, Chapter II). However, although something in the recirculating systems elicited a change in shell microstructure, the relative health of the animals did not seem to have an effect. Water temperature itself also did not appear to affect shell microstructure.

The only clear departure, found in these experiments, from this seemingly actively maintained ratio of layer thicknesses was attained in snails raised in the presence of crabs (ANOVA Table III-5; Figure III-4). This response involved an increased secretion of prisms, while the thickness of the inner crossed lamellar layer remained fairly constant. An explanation for this response does not

seem immediately apparent: both structures have comparable tensile and bending strengths (Taylor & Layman, 1972; Currey & Taylor, 1974; Currey, 1976), crossed lamellae have a higher resistance to crack propagation (Currey & Kohn, 1976), crushing (Taylor & Layman, 1972; Currey, 1976), and abrasive forces (Gabriel, 1981), and prisms are more resistant to chelating agents and protease treatments (Gabriel, 1981) (see Table III-8 for a summary of relative mechanical properties). Further, as previously discussed, because of the relatively high organic content of prismatic structure, prisms should be more expensive to secrete than crossed lamellae. Although food availabilities alone elicited no significant change in shell microstructural composition, the response of the snails to the presence of crabs was not as pronounced in individuals maintained at a reduced food availability (Table III-5) as it was in those raised with full food. The purpose of an increased secretion of a possibly more expensive microstructural layer by snails maintained in the presence of crabs is not clear.

The production of highly organized structures such as crossed lamellae may be limited by depositional rate (Vermeij & Currey, 1980). The results discussed above appear to support the concept of such a limitation. The variation in crossed lamellar layer thickness among food treatments could reflect differing growth rates. The lack of variation between crab exposure treatments at both 33% and 100% food could represent a maximal rate of crossed lamellar deposition at each food availability. Additional shell thickening in such cases was provided by an increased deposition of prismatic structure in snails raised in the presence of crabs. Further, shell

Table III-8. A comparison of the mechanical properties of simple prismatic versus crossed lamellar shell microstructures.

Mechanical property	Definition of property	Simple Prisms vs. Crossed lamellae	Source
Tensile strength	Force required to fracture a material undergoing elongation (Force/Area)	Approximately equal	Currey & Taylor, 1974; Currey, 1976
Compressive strength	Force required to fracture a material undergoing compression (Force/Area)	Approximately equal	Currey & Taylor, 1974
Bending strength	Force required to fracture a material loaded into 3-point bending (Force/Area)	Approximately equal	Currey & Taylor, 1974
Crack propagation	Ability of a material to resist propagation of an existing crack	Crossed lamellae higher	Rhoads & Lutz, 1980
Elasticity	Ability of a material to temporarily deform when placed under a load (Stress/Strain)	Approximately equal	Currey & Taylor, 1974; Currey, 1976
Plasticity	Ability of a material to permenantly deform, but not fracture under a load (Stress/Strain)	Prisms higher	Wainwright *et. al.*, 1976
Hardness	Ability of the surface of a material to resist deformation from a single force acting perpendicularly to the surface	Crossed lamellae higher	Currey, 1976
Abrasion resistance	Ability of a material to resist weight loss due to abrasive forces	Crossed lamellae higher	Gabriel, 1981
Acid resistance	Ability of a material to resist weight loss due to treatment with HCl	Approximately equal	Gabriel, 1981
Resistance to E.D.T.A.	Ability of a material to resist weight loss due to treatment with a chelating agent, E.D.T.A.	Prisms higher	Gabriel, 1981
Protease resistance	Ability of a material to resist weight loss due to treatment with a non-specific protease	Prisms higher	Gabriel, 1981

repair data (Palmer, 1983) from *Searlesia dira*, a temperate neogastropod composed entirely of crossed lamellae (Gratto, unpubl.), versus *Thais lamellosa* supports the concept of a limited rate of crossed lamellar deposition.

An inverse relationship between spiral shell growth and crossed lamellar layer thickness must be established to validate this hypothesis. In a simple overview, such a pattern between spiral shell growth and crossed lamellar layer thickness appears valid: the slower growing snails of the 33% food availability, correspondingly, secreted a thicker crossed lamellar layer. When examined more closely, however, this relationship becomes clouded. Spiral shell growth differed significantly between the crab exposure treatments of snails fed at both 33% and 100% availabilities, although crossed lamellar composition remained similar (ANOVA Table III-5, Figure III-4). Snails of the 67% and 100% food availabilities differed significantly in crossed lamellar layer thickness, while spiral growth did not vary (ANOVA Table III-4, means Table III-2). The results observed in this paper, therefore, may not be explained simply as a result of a limited rate of crossed lamellar deposition.

The higher organic content of prisms lends an increased plasticity to this layer (Wainwright *et al.*, 1976). Although both prisms and crossed lamellae have similar bending strengths, part of the strength of the prismatic layer is derived from this higher plasticity because of an increased ability to absorb energy before fracture (Wainwright *et al.*, 1976). The addition of a relatively non-plastic layer (ie. crossed lamellar) to a plastic layer (ie. prisms) may result in a reduction of the plasticity of this latter layer,

lowering its bending strength. If the relative proportion of this non-plastic layer is reduced, it follows that its influence on the outer or distal surface of the plastic layer is also reduced. In shells composed of two layers similar in properties to the shells of *Thais lamellosa*, a reduction of the proportion of the inner, relatively non-plastic layer has the effect of lowering the neutral axis (the plane of section at which strain is absent) of the cross-section of the shell, towards the inner shell surface (Byars & Snyder, 1975). Figure III-9 illustrates the approximation of the neutral axis of shell sections differing in relative thickness of the two microstructural layers, but with similar absolute thicknesses. Diagram B (Figure III-9) represents a shell from a snail raised in the presence of crabs relative to Diagram A. The neutral axes were determined by first approximating the initial bi-layer shell sections to uni-layer (prismatic) shell sections of similar mechanical properties. Because stress (force/unit area) remains constant on both the inner and outer surfaces of the shell, the proportion of material of the uni-layer sections must remain constant on either side of the neutral axis (Figure III-9, diagrams i, ii) (Byars & Snyder, 1975). . The amount of strain (proportional to the amount of deformation of the structure) is directly proportional to the distance of the surface from the neutral axis. A lowering of the neutral axis, towards the inner surface of the shell, as indicated for snails with a reduced proportion of crossed lamellae (Figure III-9), would increase the strain on the outer, more plastic shell surface, and decrease the strain on the inner, relatively non-plastic shell surface. If the shell was completely composed of either layer, the

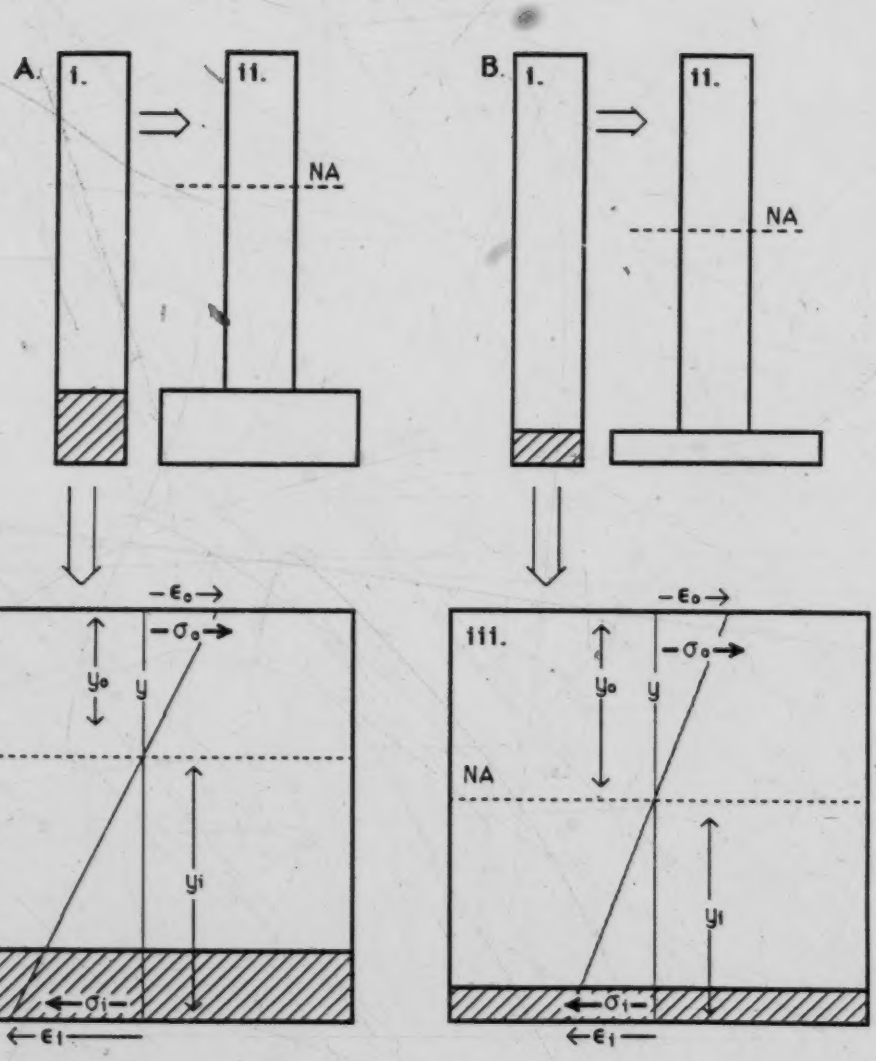
Figure III-9.

Diagrammatic view of the calculation of the neutral axis (NA) and the approximation of force vectors with varied relative thicknesses of crossed lamellar structure. The total proportion of crossed lamellar structure to prismatic was increased in these diagrams over actual natural proportions. Diagram A represents a cross-section of a shell raised in the absence of crabs, and B represents a shell of a snail raised in the presence of crabs.

i. Diagrammatic view of the cross-sections of bi-layered shells A and B.

ii. Diagrammatic view of the method of estimating the new neutral axis and uni-layer sections, arbitrarily assuming the plasticity of prisms to be three times that of crossed lamellae (Byars & Snyder, 1975).

iii. Diagrammatic view of the relative forces acting on the inner and outer shell surfaces of both the "no-crab" (A) and the "crab" (B) shell simulations (Wainwright *et. al.*, 1976).



y = total shell thickness = $y_o + y_i$
NA = neutral axis
σ = stress = force/unit area
ϵ = strain $\propto$ amount of deformation
□ = Prismatic structure
▨ = Crossed lamellar structure

$\sigma_i = \sigma_o$ (at surface)
$\epsilon_i \propto y_i$
$\epsilon_o \propto y_o$

neutral axis would remain in the centre of the cross-section, and the strain forces would be equal on both the outer and inner shell surfaces. The increased secretion of prismatic versus crossed lamellar structure, therefore, may be an attempt to reduce a detrimental influence of crossed lamellae on the bending strength of the outer surface of the shell.

The secretion, in the presence of crabs, of apertural teeth composed essentially of prisms would further emphasize this response. Apertural teeth secreted by adult *Thais lamellosa*, collected from sites both with and without crab influence, have been found to be generally composed entirely of crossed lamellae (Figure III-3). These latter apertural teeth are most likely representative of food limitations and growth stoppages, as the outer prismatic layer is not involved in their composition. On the other hand, the composition of both types of apertural teeth could merely reflect the state of their secretion with respect to the growth rate of the outer shell lip.

If, indeed, this inner layer of aragonitic crossed lamellae has a detrimental effect on the bending strength of the outer surface of the shell, its function is placed in question. The presence of this layer may reflect tropical ancestry: the calcitic outer layer possibly having evolved in temperate regions in response to the higher solubility of aragonite at decreased water temperatures. The crossed lamellar layer may also reflect an adaptation against metabolites or other chemicals which may come in contact with the inner shell surface. Crossed lamellar structure, however was found to be no more resistant than prisms to acids, and less resistant to

both chelating agents and protease treatments (Table III-8) (Gabriel, 1981).

The crossed lamellar layer is more resistant to abrasive forces than prismatic structure (Gabriel, 1981). Because this layer is located on the inner surface of the shell, however, it would provide protection from external abrasive forces only if the prismatic layer was completely eroded. Across the body whorl the crossed lamellar layer is so thin that any protection from external abrasion here would be minimal, except, perhaps, as a last barrier to bacterial or viral attack. The crossed lamellar layer appears to be secondarily secreted, as the proportion of crossed lamellae to prismatic structure increases towards the apex of the shell (Figure III-2,8). In adult snails, the apical region of the shell is the region in which external abrasion would be most prominent. Furthermore, Geller (1982) attributed the secondary apical deposition of crossed lamellae in *Tegula funebralis*, an intertidal archaegastropod, to be a response to heavy shell apical erosion. In field conditions, however, shell erosion, while prevalent in *Tegula funebralis*, was not observed to be as marked in *Thais lamellosa* (pers. obs.).

The presence of sublayers of radial and concentric crossed lamellae serve to increase shell resistance to crack propagation (Currey & Kohn, 1976). Across the body whorl, the crossed lamellar layer is too thin to provide much protection against crushing forces, but the increased number of alternating sublayers of radial and concentric crossed lamellae towards the shell apex, would contribute greater strength to the upper whorls of the shell. It is doubtful that alternating the orientations of the sublayers of

crossed lamellae would have much effect on its ability to resist abrasion.

All major superfamilies within the meso- and neogastropods have independently evolved the secretion of shells either wholly or partially composed of crossed lamellae (Currey & Taylor, 1974). Similarly, in temperate regions, most meso- and neogastropods are composed of inner crossed lamellar and outer prismatic layers, as found in *Thais lamellosa*, with the remaining entirely composed of crossed lamellae (pers. obs.). The presence of crossed lamellae on the inner surface of the shells of such species appears to transcend their varied habits and habitats. That such similar pressures from erosive and shell breaking forces could act to such a degree on all these species as to influence this apparently fundamental shell microstructural composition is questionable. Perhaps the inner layer, instead, serves to protect the shell from the presence or movement of the animal itself. The presence of nodes or "pearls" of nacre have been observed inside the aperture of species such as *Tegula funebralis* and *Astraea gibbosum* (archaegastropods which secrete nacre as an inner shell layer) on several occasions (pers. obs.). The presence of such nodes suggests that debris may enter the shell aperture and become trapped between the shell and mantle, perhaps acting as an abrasive on the shell with snail movement. Because of the greater ability of crossed lamellar structure to resist abrasion, the presence of crossed lamellae on the inner surface of the shell may also reflect a protection of the delicate tissues of the animal itself from abrasion against an eroded surface. Either above theory of prevention of internal abrasion, however, does

not explain the function of the secondary secretion of crossed lamellae on the internal surface of the shell. Such secondary secretion, however, does not occur consistently across species. Some snails, such as those of the genus *Conus*, have been found to dissolute shell material from their internal surfaces (Kohn *et al.*, 1979). Perhaps the secondary shell secretion in *Thais lamellosa* reflects a secondary function of resistance to either external abrasive forces or to shell breaking forces exerted on the upper whorls of the shell.

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Chapter IV.
General Summary

Similar morphological responses were observed in snails raised under a variety of treatments (limited food availability, crab presence, and increased temperatures): decreased growth in shell length, decreased body growth, and decreased spiral growth. Snails raised in the presence of crabs and at increased water temperatures also increased in shell thickness. All are responses which are to be expected from snails growing in less than ideal conditions. In snails raised with the threat of possible crab predation, the benefits to increasing shell thickness are self-evident. The function of shell thickening in response to elevated water temperatures is less obvious. Possibly this thickening represents a fundamental predator avoidance response associated with slower growth.

Despite possible differential costs of shell layer secretion, little microstructural variation was observed between food availability treatments, although shell and body growth varied significantly. Water temperature differences, also, did not induce a difference in the proportional deposition of the two microstructural layers, although the design and conduction of the recirculating systems of this experiment did appear to cause a change in shell microstructural proportions. Shell and body growth varied significantly among water temperature treatments. The only clearly defined microstructural response observed in these experiments was in response to the scent of crabs consuming conspecific snails.

Many of the shell morphological responses associated with predators have been attributed to decreased food consumption. While morphological variations were similar between reduced food availability and crab-presence treatments, shell microstructural composition differed. Snails raised at the three food availabilities varied with respect to individual microstructural layer secretion, but produced both layers in similar proportions. At each of the two food availabilities studied in the crab-exposure experiment, snails raised in the presence of crabs did not vary in crossed lamellar layer secretion, but increased in both absolute and relative thickness of the layer as opposed to snails raised in the absence of crabs.

Apertural teeth of juveniles raised in the presence of crabs were of a different microstructural composition than those of field collected adults from sites without the influence of large crabs. Snails raised in the presence of crabs secreted apertural teeth essentially composed of prisms, while teeth produced by field-collected adults were entirely of crossed lamellae. The secretion of apertural teeth found in these latter cases is presumed to be the result of food limitations and/or growth stoppages. None of the food limited, laboratory-raised juveniles of these experiments initiated the development of apertural teeth.

The apparent preferential secretion of this relatively energetically expensive prismatic microstructure may reduce possible detrimental effects of the inner layer on the bending strength of the outer surface of the shell. The secretion of apertural teeth essentially composed of prisms would further reduce any effect of the inner layer on the bending strength of the shell.

Possible functions of this inner crossed lamellar layer include i. increased resistance to crack propagation, ii. increased resistance to abrasion from external sources, and iii. increased resistance to abrasion from internal sources. Because of the prominent evolutionary trends towards increased secretion of crossed lamellae within the class Gastropoda, the latter explanation could be the most valid.

Whatever the function of the inner crossed lamellar layer, it is important to note that, with the exception of the crab-influenced snails, the proportional deposition of both layers remained constant throughout the food availability treatments, and within snails from all sites studied. Snails from the temperature experiment secreted a relatively higher proportion of crossed lamellar to prismatic structure, although the cause for such a change could not be determined. It is probable that something was limited, something necessary for the secretion of the more organically-rich prismatic layer, in the recirculating system of this experiment. Surprisingly, however, the proportion of crossed lamellar to prismatic structure remained constant across all temperature treatments, although the relative health of animals appeared to vary among treatments. In both of these experiments, shell morphology changed markedly. The proportional secretion of both microstructural layers appears to be actively maintained, regardless of food availability, water temperature, snail morphology, and, to at least some extent, animal health.

All snails from all sites, regardless of relative wave exposures and predation pressures, demonstrated similar responses, both in

shell morphology and shell microstructure, to the stimuli presented here. The degree of response to any of the stimuli did not vary between sites, although Argyle Creek snails were significantly less likely to develop apertural teeth than those snails from the remaining four sites. All snails, however, did maintain the basic shell morphologies of their parent populations throughout all treatments. Features of shell morphology, such as shell thickness and apertural teeth appear to be environmentally influenced, while features such as external shell sculpture and colour, as well as the degree of the morphological response, appear less subject to environmental modification.

Appendix 1
Shell microstructural types

Prismatic structure.

The first order prisms are oriented parallel with respect to each other, with discrete boundaries.

a. Simple prisms. The second order prisms comprising the first order prisms are oriented in neither a spherulitic nor a composite manner. The boundaries of adjacent first order prisms are well defined.

i. Regular. Each first order prism is essentially equidimensional (Figure 1-1A).

ii. Irregular. A cross section of the first order prisms reveals them to be of variable dimensions with irregular boundaries (Figure 1-1B).

b. Spherulitic prisms. The second order prisms radiate outward in all directions, toward the depositional surface, from a common mid point.

c. Composite prisms. The second order prisms radiate outward in all directions, toward the depositional surface, from a common longitudinal axis of the first order prism.

Spherulitic structure.

The elongate second order prisms radiate three-dimensionally from a common point, forming spherical to subspherical aggregates (Figure 1-1C).

Laminar structures.

The first order prisms are flattened and sheet-like. They are generally oriented parallel to, or approximately parallel to, the depositional surface of the shell.

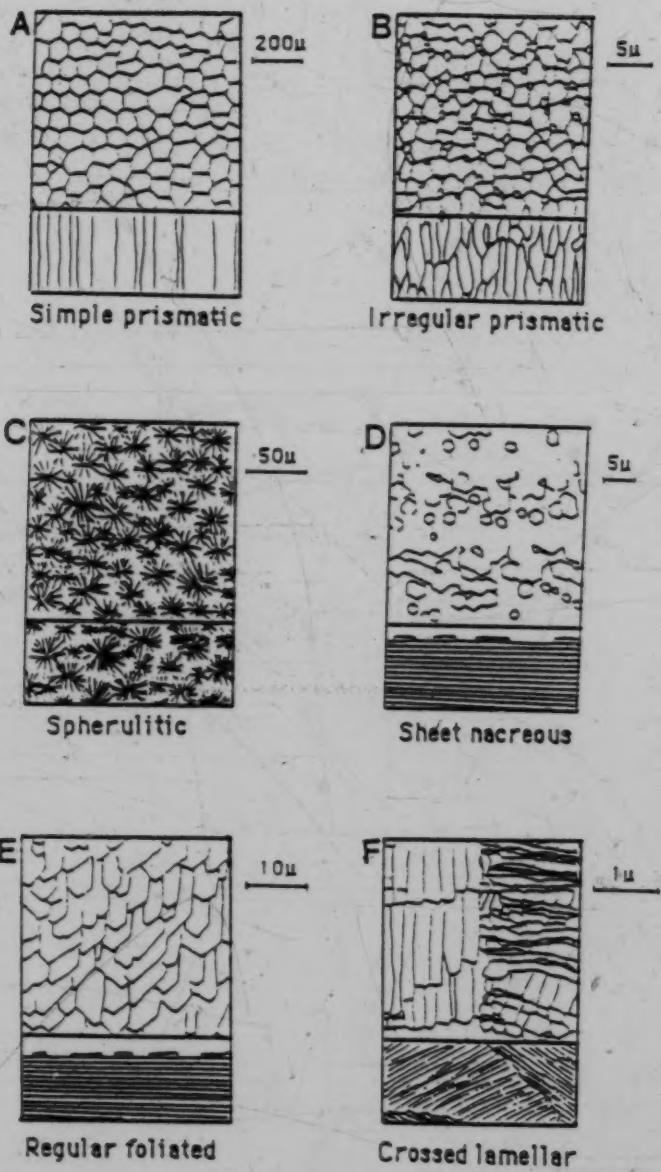
a. Nacre. This microstructure is wholly aragonitic. The first order units are polygonal to rounded tablets arranged in large parallel sheets (Figure 1-1D).

b. Foliated. This microstructure is generally calcitic. The first order structural units are flat or lath-like. They are arranged in parallel to adjacent sheets (Figure 1-1E).

c. Crossed lamellar. The substructural units are rods or blades, arranged in parallel fashion into aggregates, or primary lamellae. The orientation of these subunits is essentially constant within a single lamel, but adjacent lamellae generally vary in

Figure A1-1.

A diagrammatic view of some of the more common shell microstructural types (taken from Carter & Clark, 1980).


A
200μ
Simple prismatic
B
5μ
Irregular prismatic
C
50μ
Spherulitic
D
5μ
Sheet nacreous
E
10μ
Regular foliated
F
1μ
Crossed lamellar

orientation by 70 to 90 . There are only two directions of lamellar orientation in this microstructure (Figure 1-1F).

d. Complex crossed lamellar. This microstructure is similar to crossed lamellae, but there may be three or more directions of orientation of primary lamellae.

Homogeneous structures.

This microstructure consists of aggregations of irregular crystals with no clear first order structural arrangement.

Appendix 2
Method of Degree of Wave Exposure Calculation

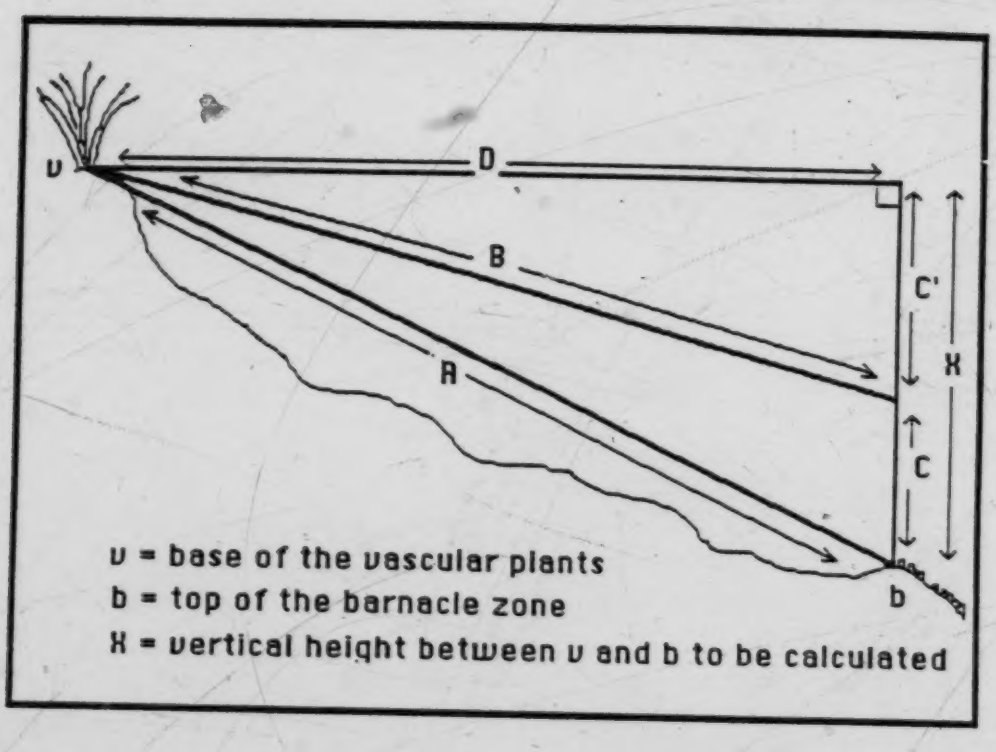
Relative degrees of wave exposure was estimated for each site by calculating the vertical distance (X) from the top of the barnacle zone (b) to the base of the vascular plants (v). This height was determined by measuring two linear distances: one (A) along the substratum from the top of the barnacle zone to the base of the vascular plants, and the second (B), similar to the first, but with the barnacle zone endpoint raised a set distance above the substratum.

A hypothetical line (D) was constructed perpendicular to the vertical line X, connecting with point v, the base of the vascular plants. X, itself, only extended from point b, the top of the barnacle zone, to line D. Line X was divided into two sections: C, the known distance along X, between lines A and B, and C', the remaining distance along X (ie. C' = X - C). These lines and their subsequent triangles, as well as the calculations for the distance X, are depicted in Figure 2-1.

Two right angle triangles were thus constructed: A, X (= C + C'), D and B, C', D. Following Pythagorean's theorum, the sum of the squared lengths of the two sides adjacent to the right angle is equal to the square of the length of the hypotenuse. Equations were derived from this theorum for the determination of side lengths for both of the above triangles. As both triangles have a single side in common, D, both equations were solved for this length, and the values substituted. The resulting single equation was then solved for C', which was subsequently used to determine the vertical

Figure A2-1.

A diagrammatic view of the wave exposure index measurements taken in the intertidal zone at all five collection sites, and the subsequent calculations of this index. v = base of the vascular plants, b = top of the barnacle zone, A, B, and C = lines measured in the intertidal zone, X = vertical height to be calculated.



Calculations.

$A^2 = (C + C')^2 + D^2$ $\qquad$ $B^2 = (C')^2 + D^2$

$D^2 = A^2 - (C + C')^2$ $\qquad$ $D^2 = B^2 - (C')^2$

$$A^2 - [C^2 + 2CC' + (C')^2] = B^2 - (C')^2$$

$$A^2 - C^2 - 2CC' = B^2$$

$$C' = \frac{A^2 - C^2 - B^2}{2C}$$

$$X = C + C'$$

distance X, or the height in the intertidal from the top of the barnacle zone to the base of the vascular plants.

Three sets of measurements and calculations were conducted for each site, and the mean vertical distance, X, was used as the wave exposure index.

Appendix 3

Method of Non-destructive Calculation of Dry Shell and Dry Body Weights

The calculation of dry shell and dry body weight from the measured values of weight of the snails in air and weight immersed in sea water is as follows. A set of conversion factors were established using approximately twenty five field collected individuals of a thin-shelled, highly-fluted population of *Thais lamellosa* from Dixon Island (Barkley Sound, British Columbia, Canada), and approximately twenty five individuals from a thick, smooth-shelled population from Grappler Inlet (Barkley Sound, British Columbia, Canada). All snails were randomly collected, but generally were of the subadult size range (less than 3 cm). Both populations were combined for the calculation of the conversion factors used in this paper, as i. the separately calculated conversion factors did not vary greatly between the two populations, and ii. I did not want to bias my end results and calculations by arbitrarily using the conversion factor of either a thick or thin-shelled population, or by using different conversion factors for different sites and/or treatments.

The remaining measurements and calculations were conducted as in Palmer (1982). Both air weights and immersed weights were measured on each individual from the two populations. The shells were then broken with a hammer, and the shell fragments removed from the soft body tissues. The shell and body pieces of each individual were placed into separate tared weigh boats and dried at

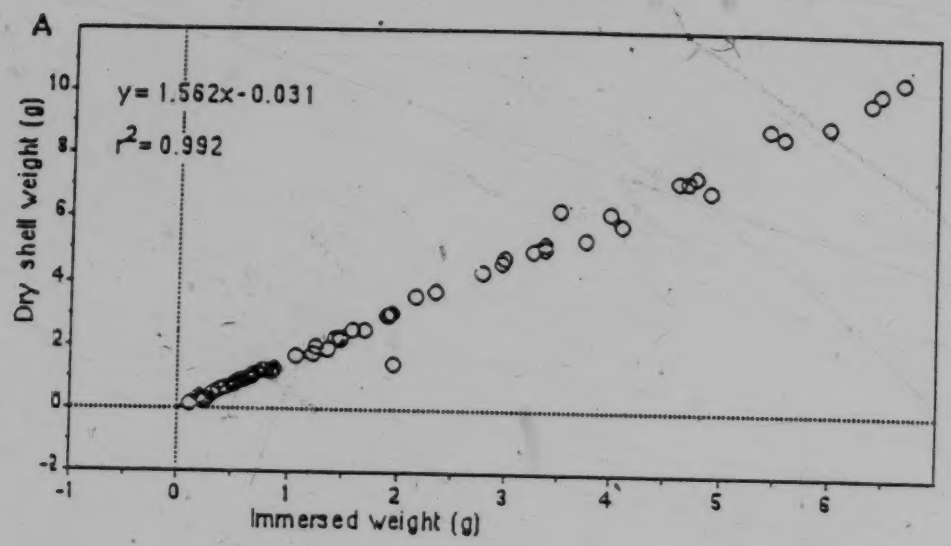
Figure A3-1.

Conversion of immersed snail weight and weight of the snail in air to dry shell and dry body weight. All the data points represented here are from two combined populations (one thick and one thin-shelled) of subadult field collected *Thais lamellosa*.

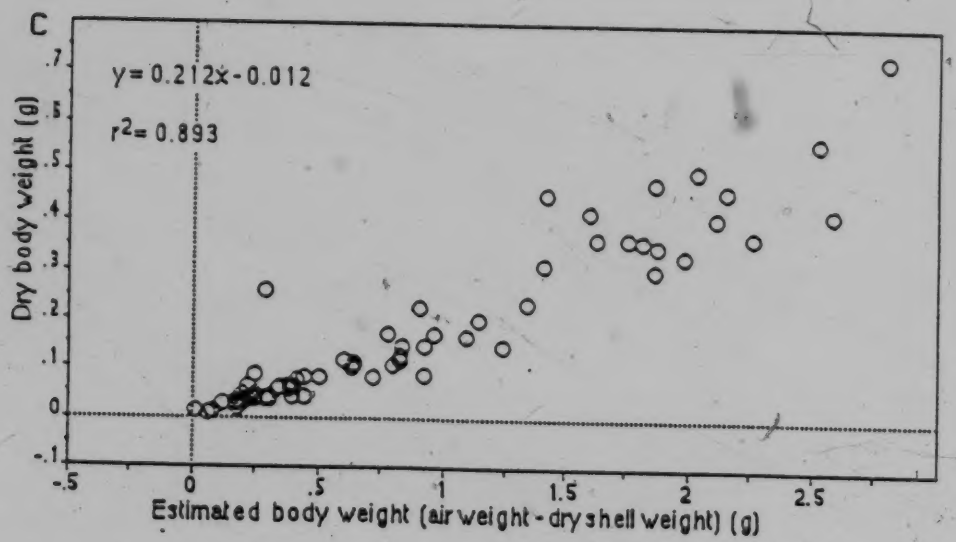
A. Regression for the calculation of dry shell weight from immersed snail weight.

B. Equation for the calculation of estimated body weight.

C. Regression for the calculation of dry body weight from estimated body weight.



B Estimated body weight = Weight of the snail in air - Dry shell weight.



40°C for a period of forty eight hours. Air weights of both the dry shell and dry body fragments were measured.

Dry shell weight plotted against immersed snail weight yielded a conversion factor of dry shell weight = 1.562•(immersed snail weight) - 0.031 (Figure 3-1A). Estimated dry body weight was calculated by subtracting dry shell weight from the weight of the snail in air (Figure 3-1B). The values of dry body weight were then plotted against estimated body weight to yield a relationship of dry body weight = 0.212•(estimated body weight) - 0.012 (Figure 3-1C).

From the use of the three equations above, dry body and dry shell weight may be estimated non-destructively from weight of the snails in air and immersed in sea water. These calculations are assumed to be reliable because of the relatively high r^2 values (0.992 and 0.893, respectively) (Figure 3-1) for both regressions used, in spite of the combination of both thick and thin-shelled populations.

APPENDIX 4

Additional scattergrams from Chapter II.

Figure A4-1.

Scattergrams of final versus initial shell lengths (cm) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

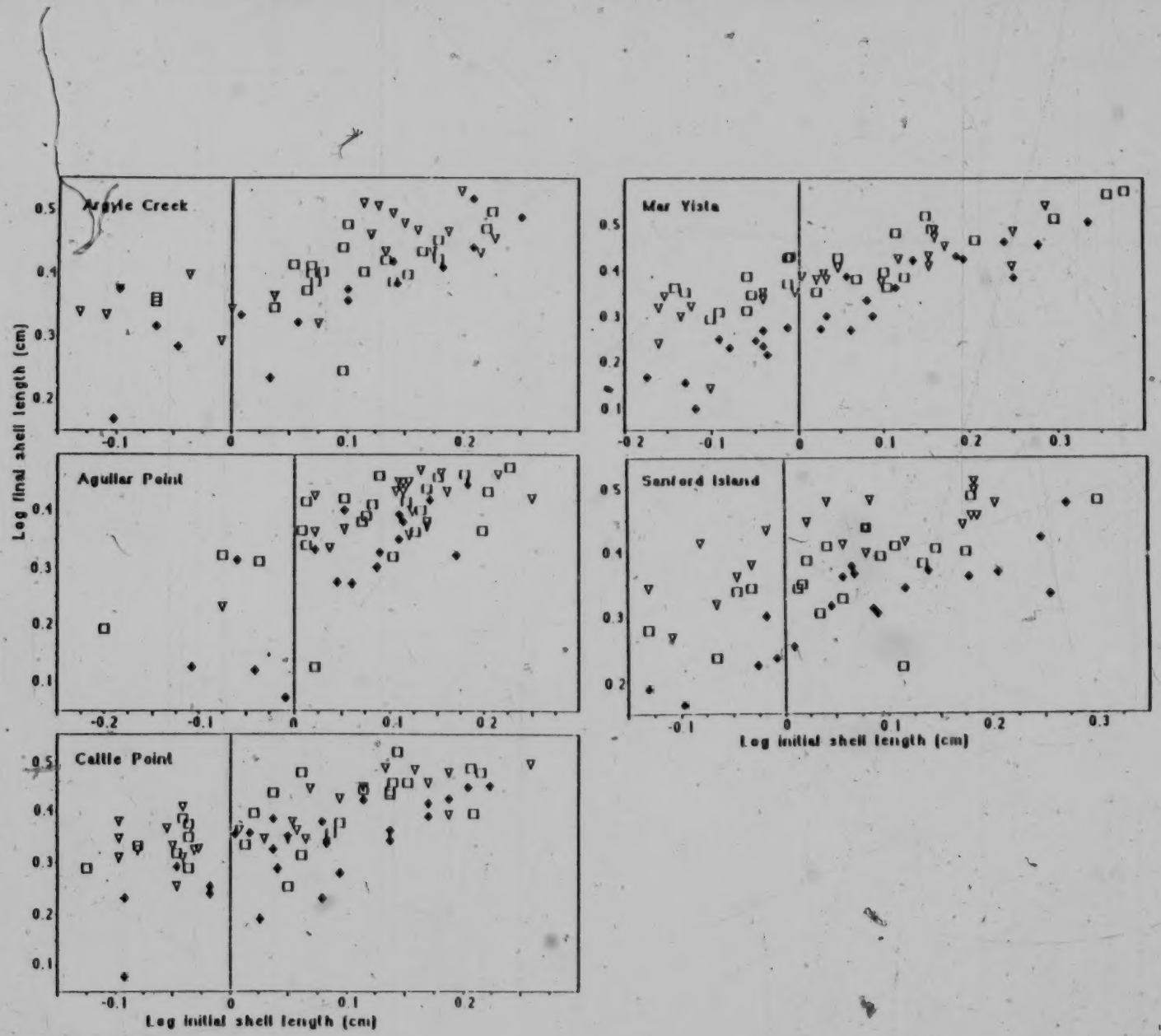

Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point
Log final shell length (cm)
Log initial shell length (cm)
Log initial shell length (cm)

Figure A4-2.

Scattergrams of final versus initial dry shell weight (g) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

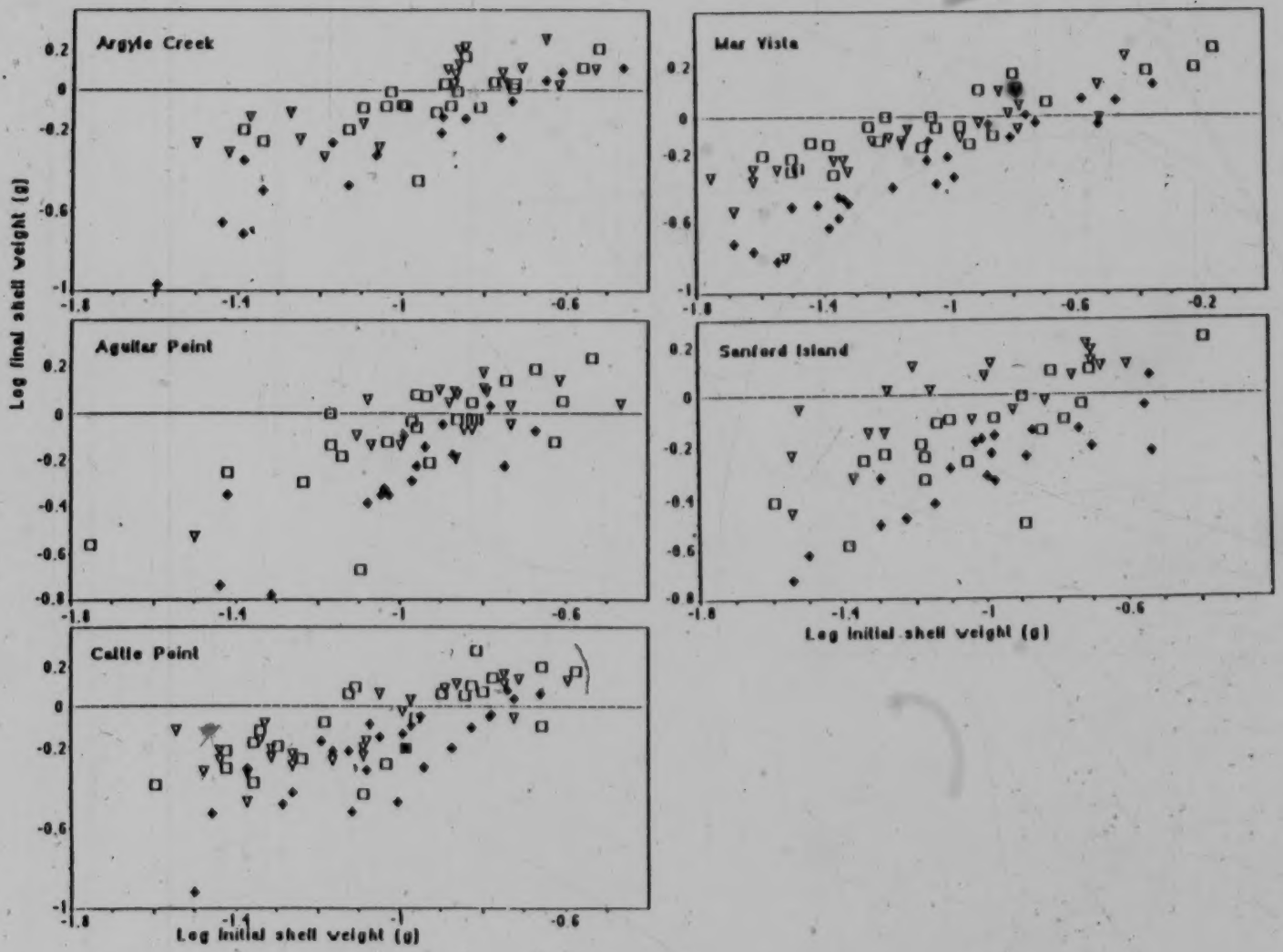

Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point
Log final shell weight (g)
Log initial shell weight (g)
Log initial shell weight (g)

Figure A4-3.

Scattergrams of final versus initial dry body weight (g) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

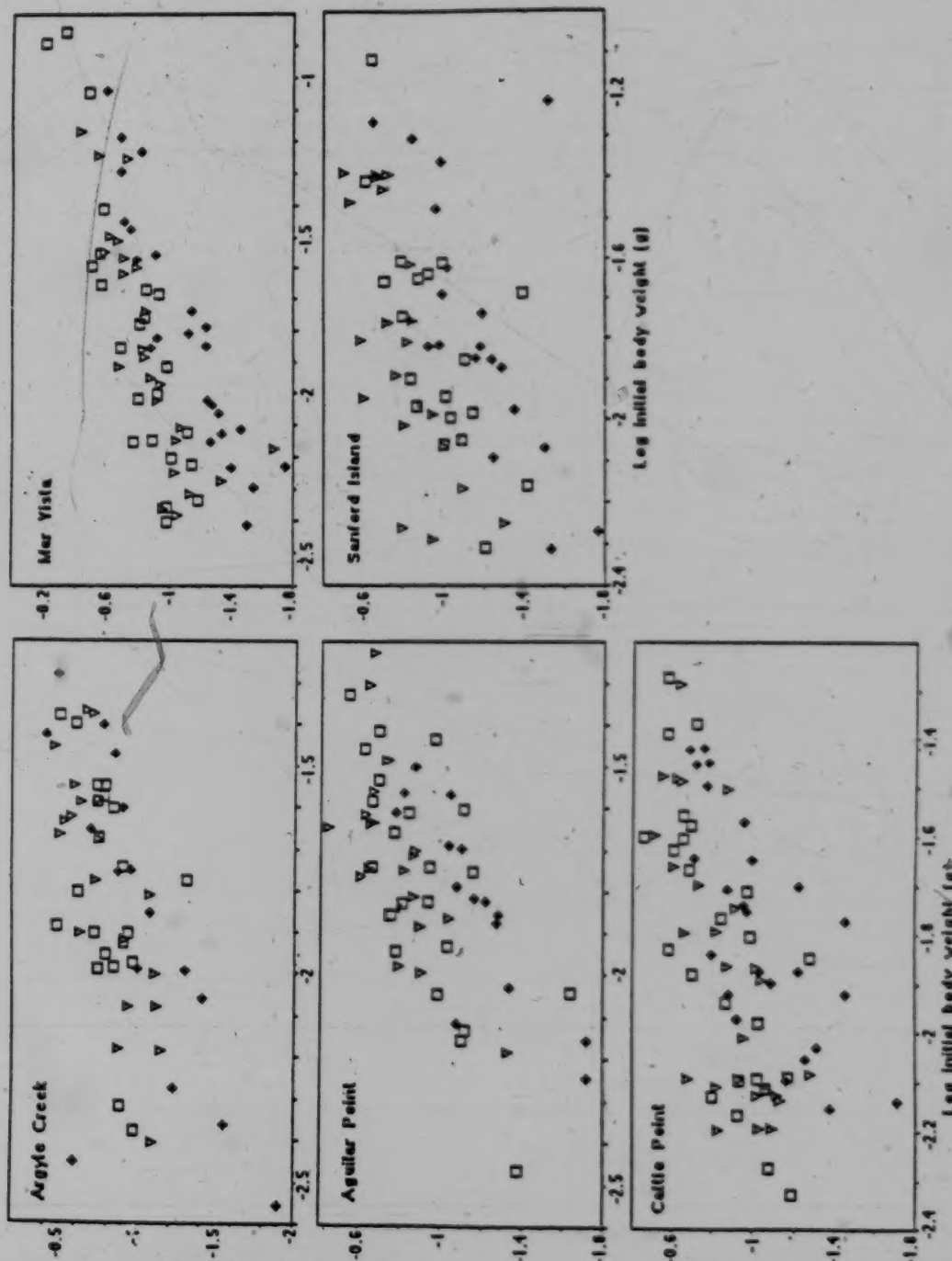

Argyle Creek
Mar Vista
Sanford Island
Aguilar Point
Cattle Point
Log final body weight (g)
Log initial body weight (g)

Figure A4-4.

Scattergrams of spiral growth (mm) versus initial shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%

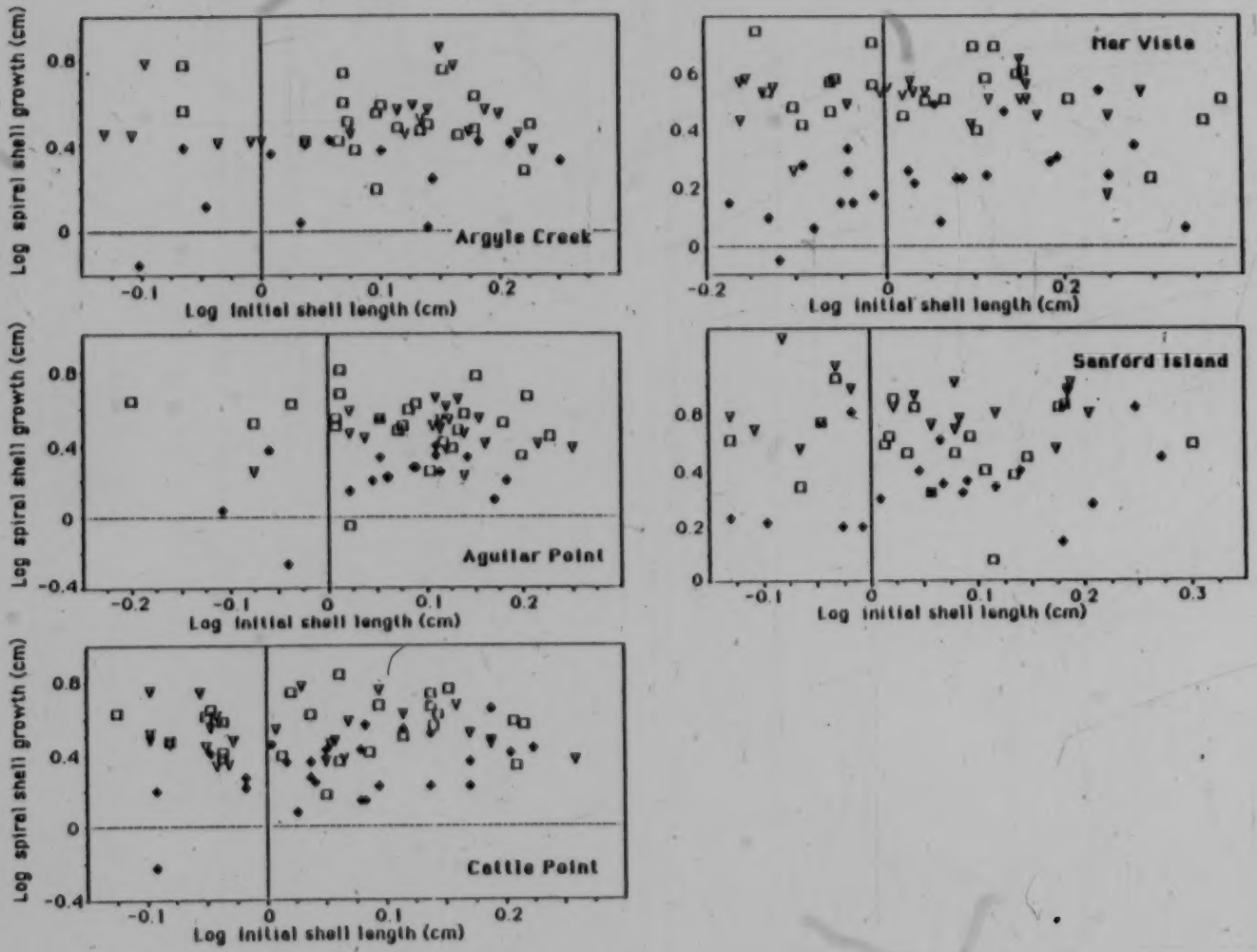

Log spiral shell growth (cm)
Log initial shell length (cm)
Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point

Figure A4-5.

Scattergrams of shell thickness (mm) versus initial shell length (cm) for juvenile *Thais lamellose* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities.

◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

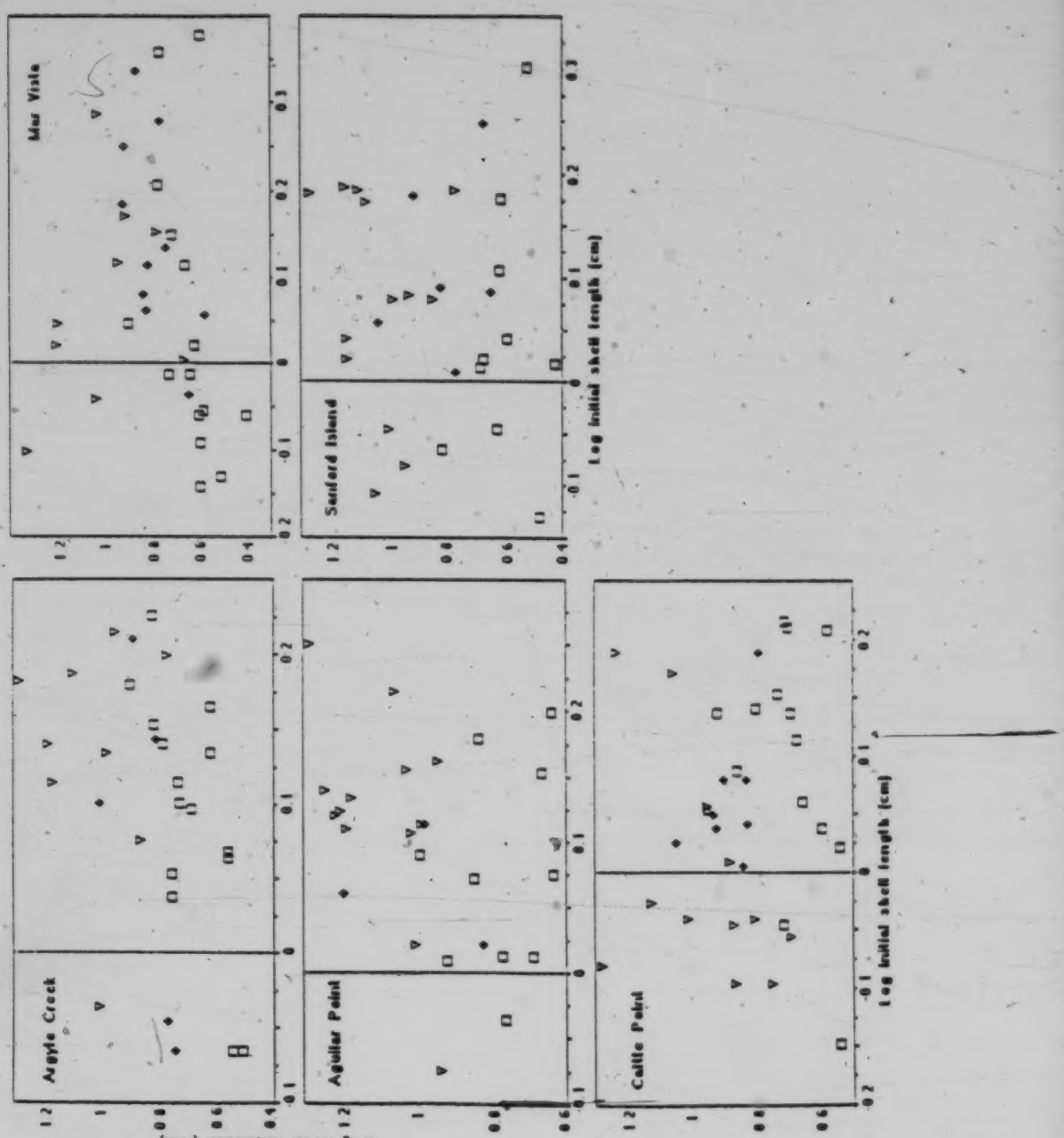
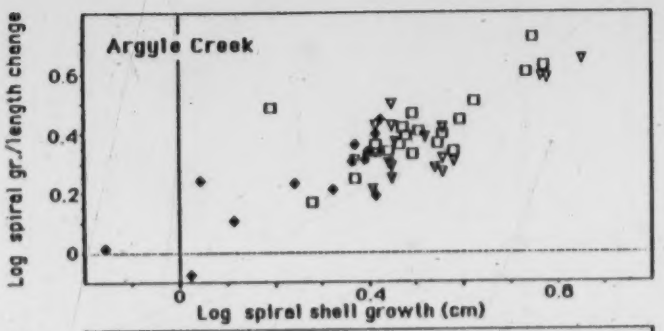
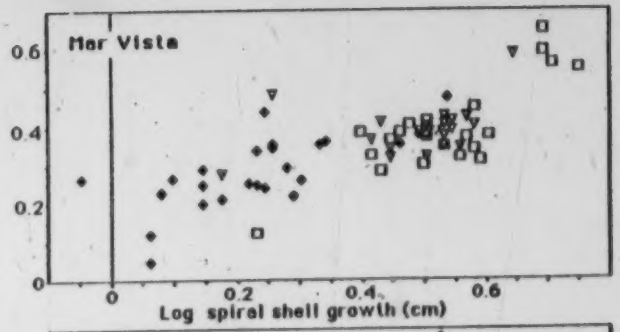
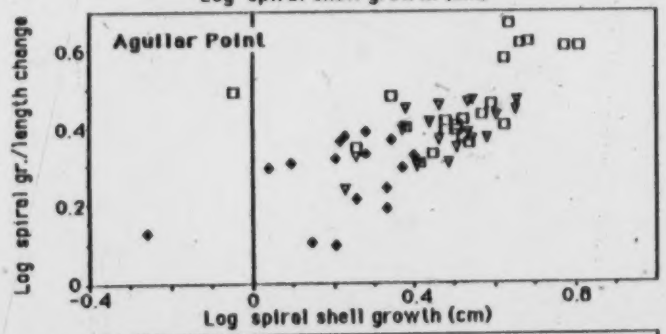

Argyle Creek
Aguilar Point
Cattle Point
Mar Vista
Sanford Island
Log shell thickness (mm)
Log initial shell length (cm)
Log initial shell length (cm)

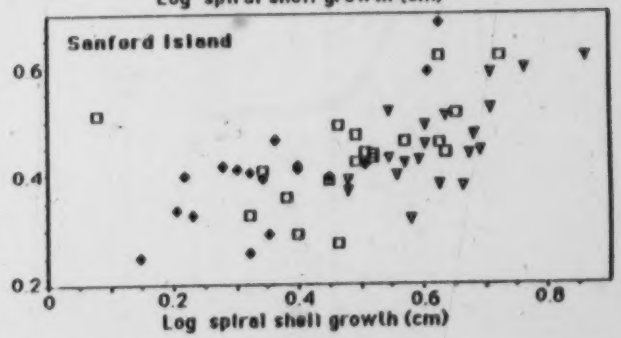
Figure A4-6.

Scattergrams of shell length change/spiral growth versus spiral growth (mm) (= translation rate) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ♦ = fed 33%, □ = fed 67%, ▽ = fed 100%.


Argyle Creek
Log spiral gr./length change
Log spiral shell growth (cm)


Mar Vista
Log spiral shell growth (cm)


Aguilar Point
Log spiral gr./length change
Log spiral shell growth (cm)


Sanford Island
Log spiral shell growth (cm)

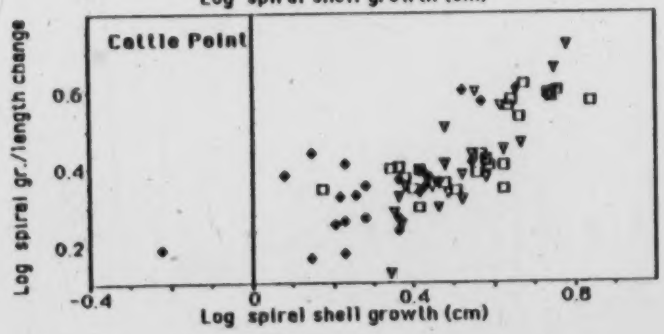

Cattle Point
Log spiral gr./length change
Log spiral shell growth (cm)

Figure 4 - 7.

Scattergrams of final versus initial shell lengths (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

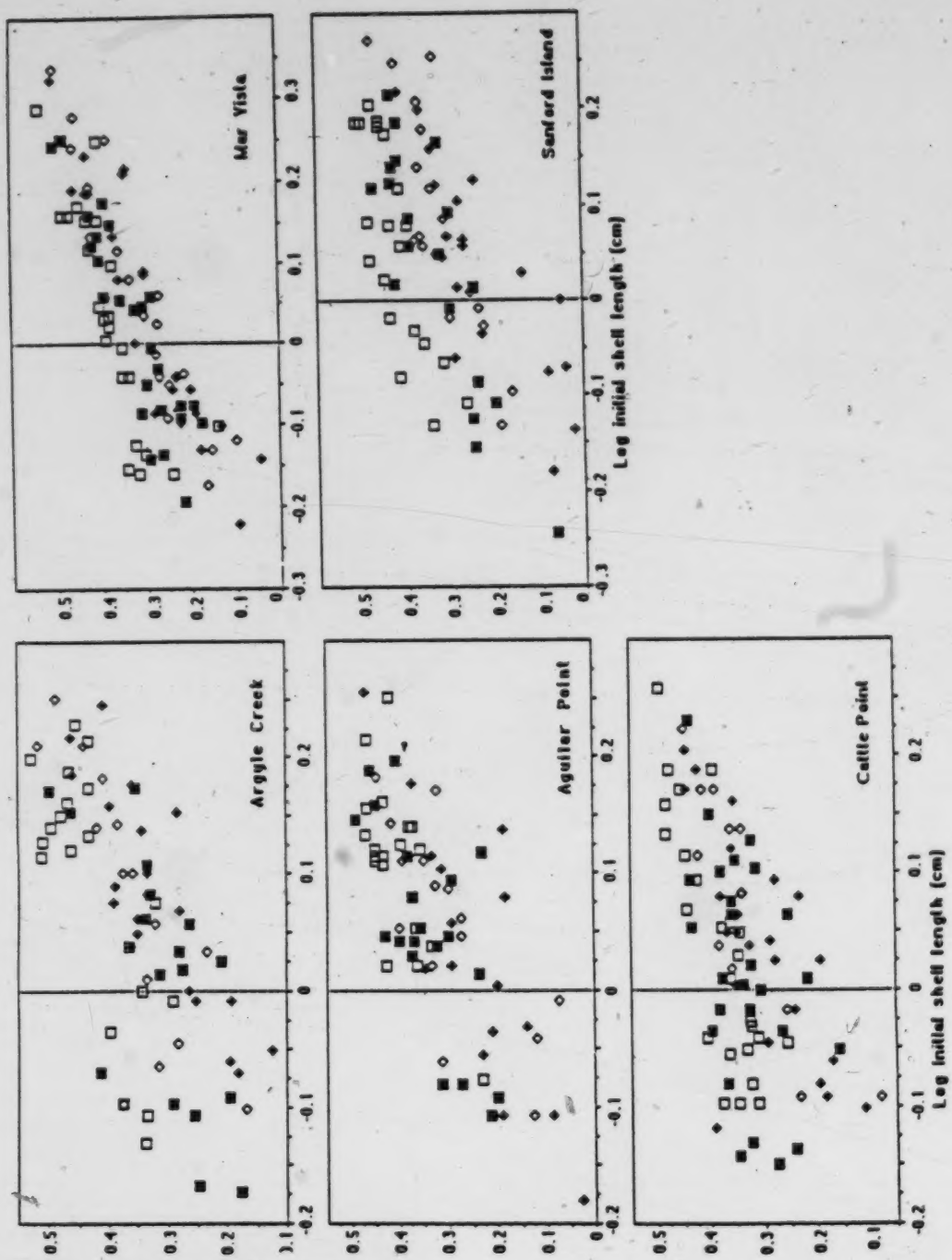

Mar Vista
Sanford Island
Argyle Creek
Aguilar Point
Cattle Point
Log initial shell length (cm)
Log final shell length (cm)

Figure A4-8.

Scattergrams of final versus initial dry shell weights (g) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

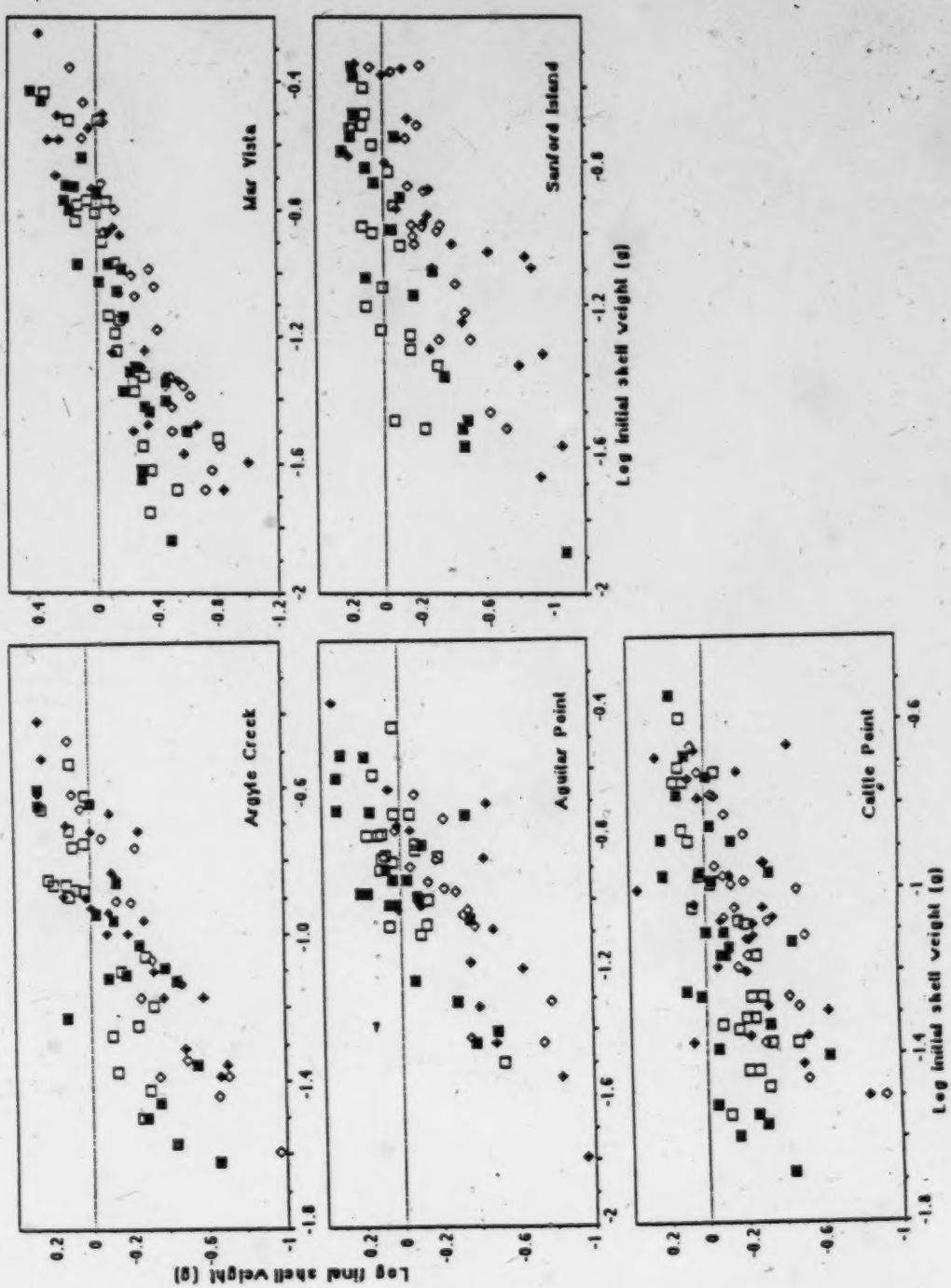

Mar Vista
Sanford Island
Argyle Creek
Aguilar Point
Calife Point
Log final shell weight (g)
Log initial shell weight (g)

Figure A4-9.

Scattergrams of final versus initial dry body weights (g) for juvenile *Thais lamellose* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

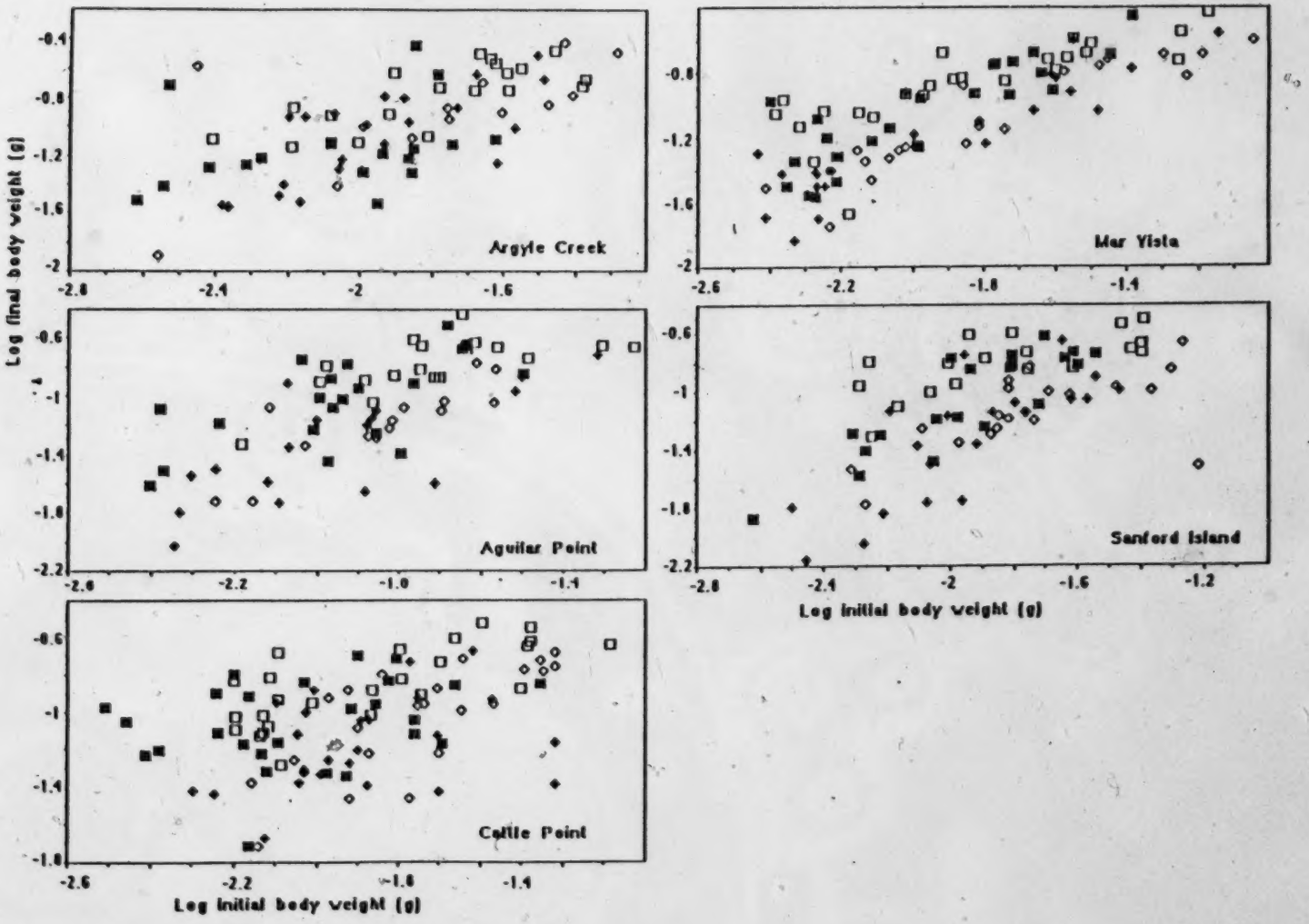

Log final body weight (g)
Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point
Log initial body weight (g)
Log initial body weight (g)

Figure A4-10.

Scattergrams of spiral shell growth (mm) versus initial shell length (cm) for juvenile *Thais lamellose* from five sites, raised in the laboratory at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

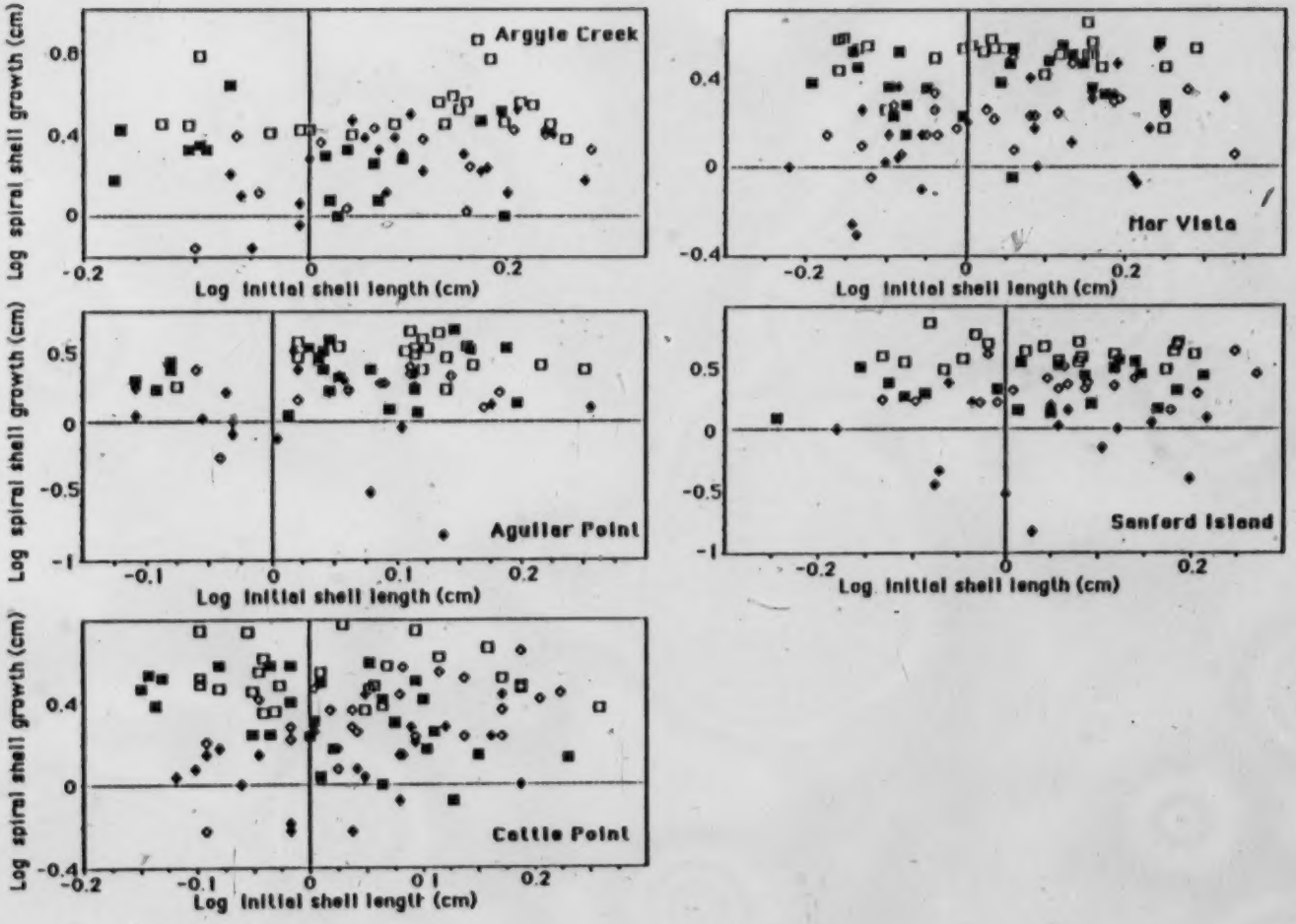

Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point
Log spiral shell growth (cm)
Log initial shell length (cm)

Figure A4-11.

Scattergrams of final shell thickness (mm) versus initial shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities.

◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

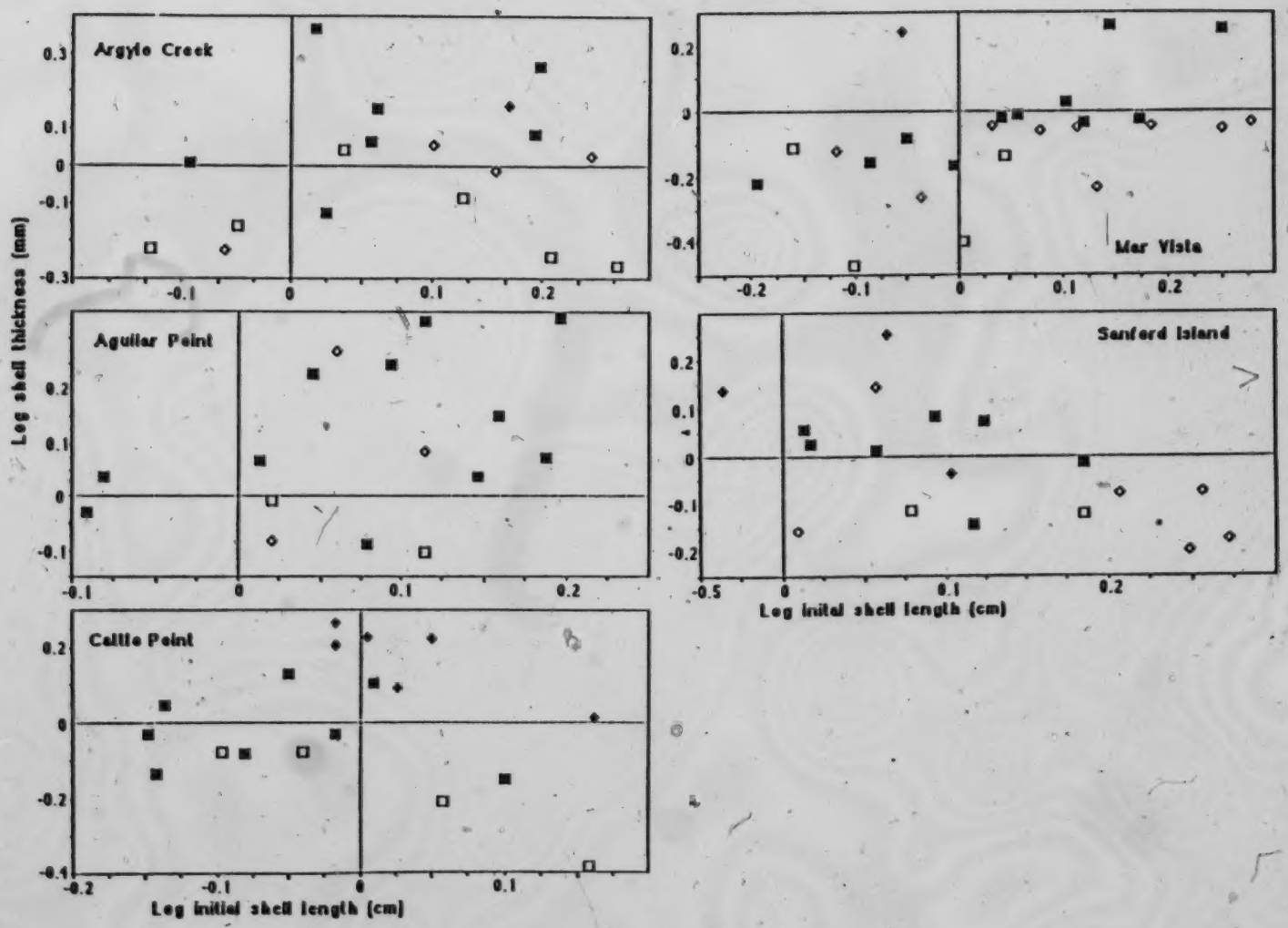

Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Callie Point
Log shell thickness (mm)
Log initial shell length (cm)
Log initial shell length (cm)

Figure A4-12.

Scattergrams of shell length change/spiral growth versus spiral growth (mm) (= translation rate) for juvenile *Thais lamellosa* from five sites, raised in the in the laboratory at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

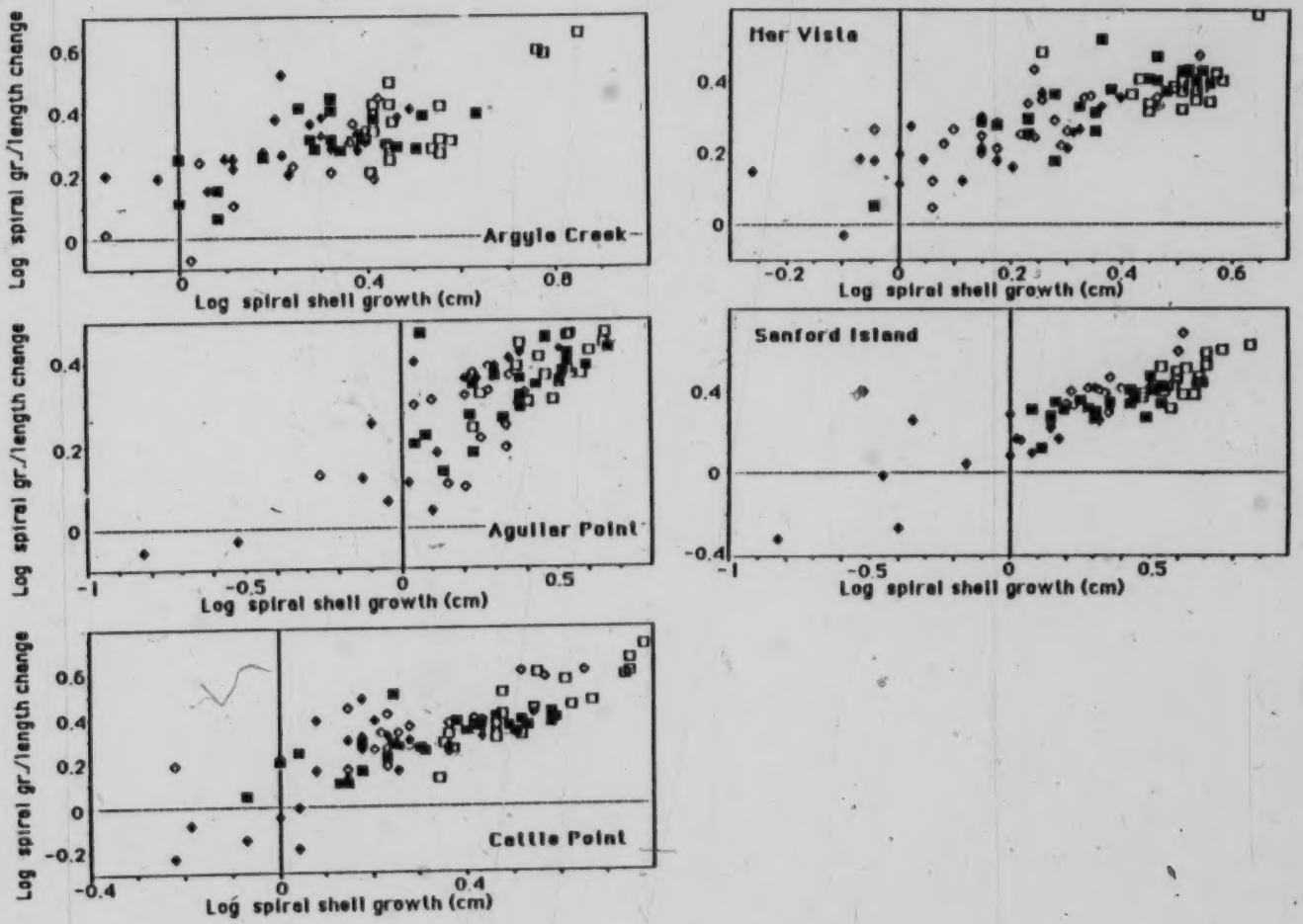

Log spiral gr./length change
Log spiral shell growth (cm)
Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point

Figure A4-13.

A.
Scattergrams of final versus initial shell lengths (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

B.
Scattergrams of final versus initial dry shell weights (g) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

C.
Scattergrams of final versus initial dry body weights (g) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

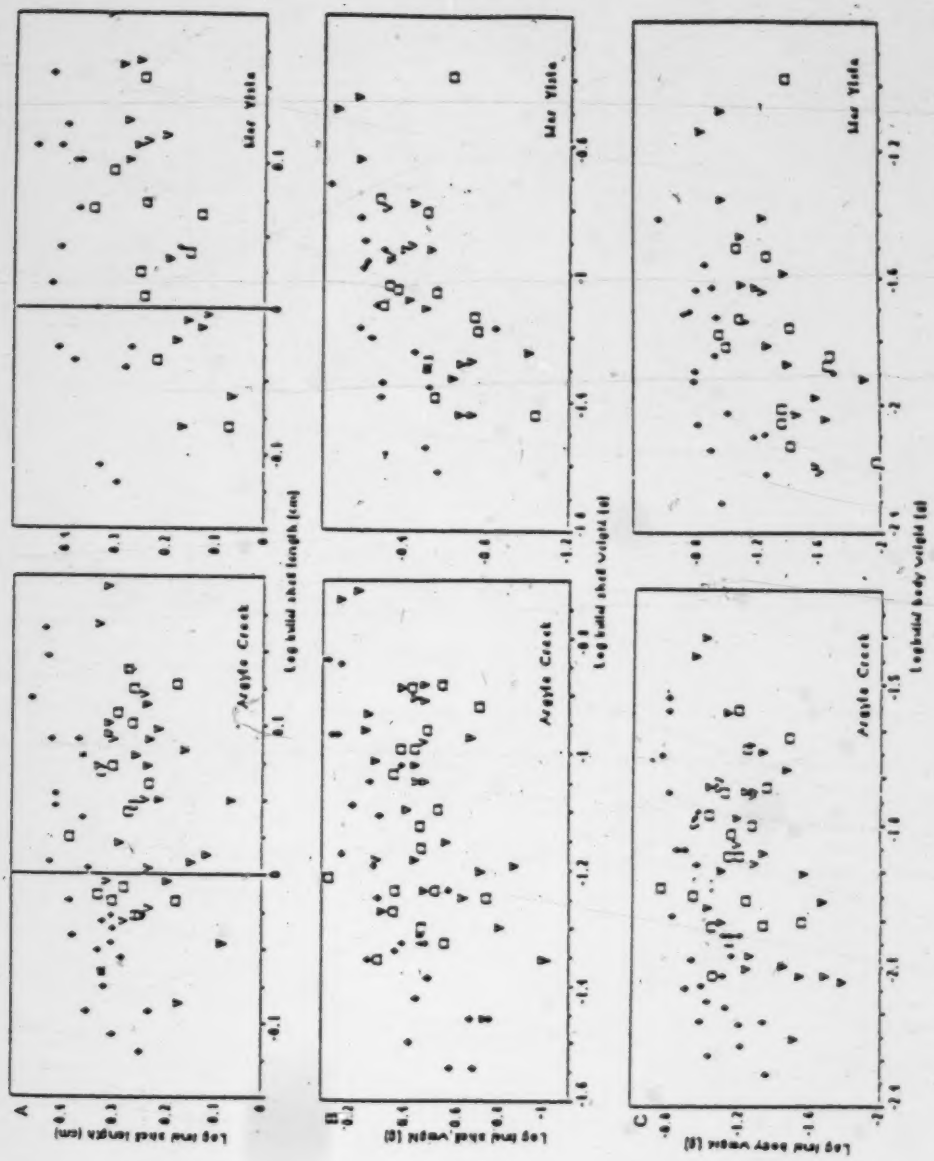

A
B
C
Log final total length (cm)
Log final total weight (g)
Log final body weight (g)
Log initial shell length (cm)
Log initial shell weight (g)
Log initial body weight (g)
Argyle Creek
Mar Vista

Figure A4-14.

A.
Scattergrams of spiral shell growth (mm) versus initial shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

B.
Scattergrams of final shell thickness (mm) versus initial shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

C.
Scattergrams of shell length change/spiral growth versus spiral growth (mm) (= translation rate) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures. ◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

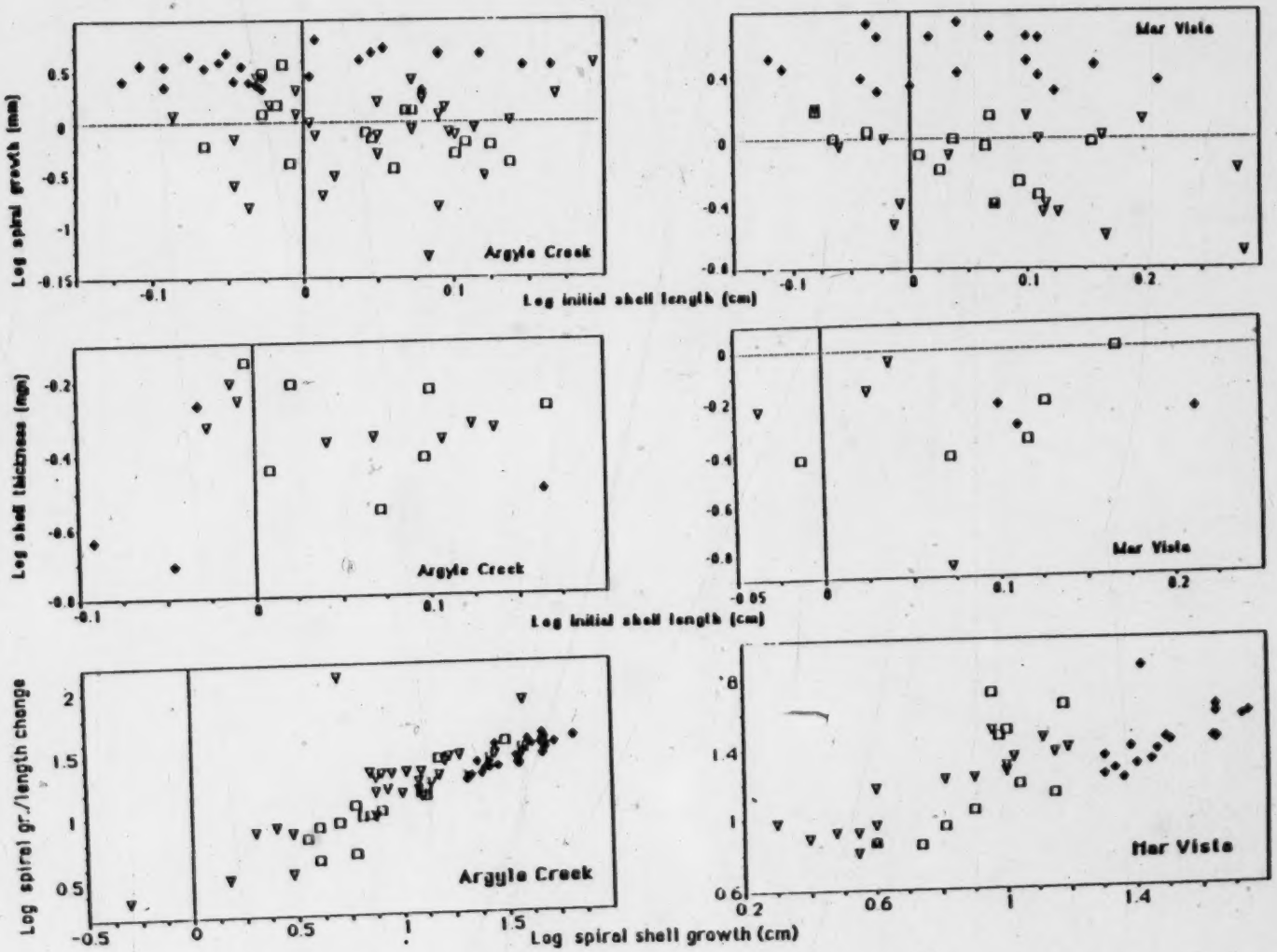

Log spiral growth (mm)
Argyle Creek
Mar Vista
Log initial shell length (cm)
Log shell thickness (mgn)
Argyle Creek
Mar Vista
Log initial shell length (cm)
Log spiral gr./length change
Argyle Creek
Mar Vista
Log spiral shell growth (cm)

Figure A4-15.

Scattergrams comparing variation among study sites with regard to log final shell length (cm) versus initial shell length (cm) at all food availabilities and crab exposures. ■ = Argyle Creek, ◇ = Aguilar Point, □ = Cattle Point, ○ = Mar Vista, ◆ = Sanford Island.

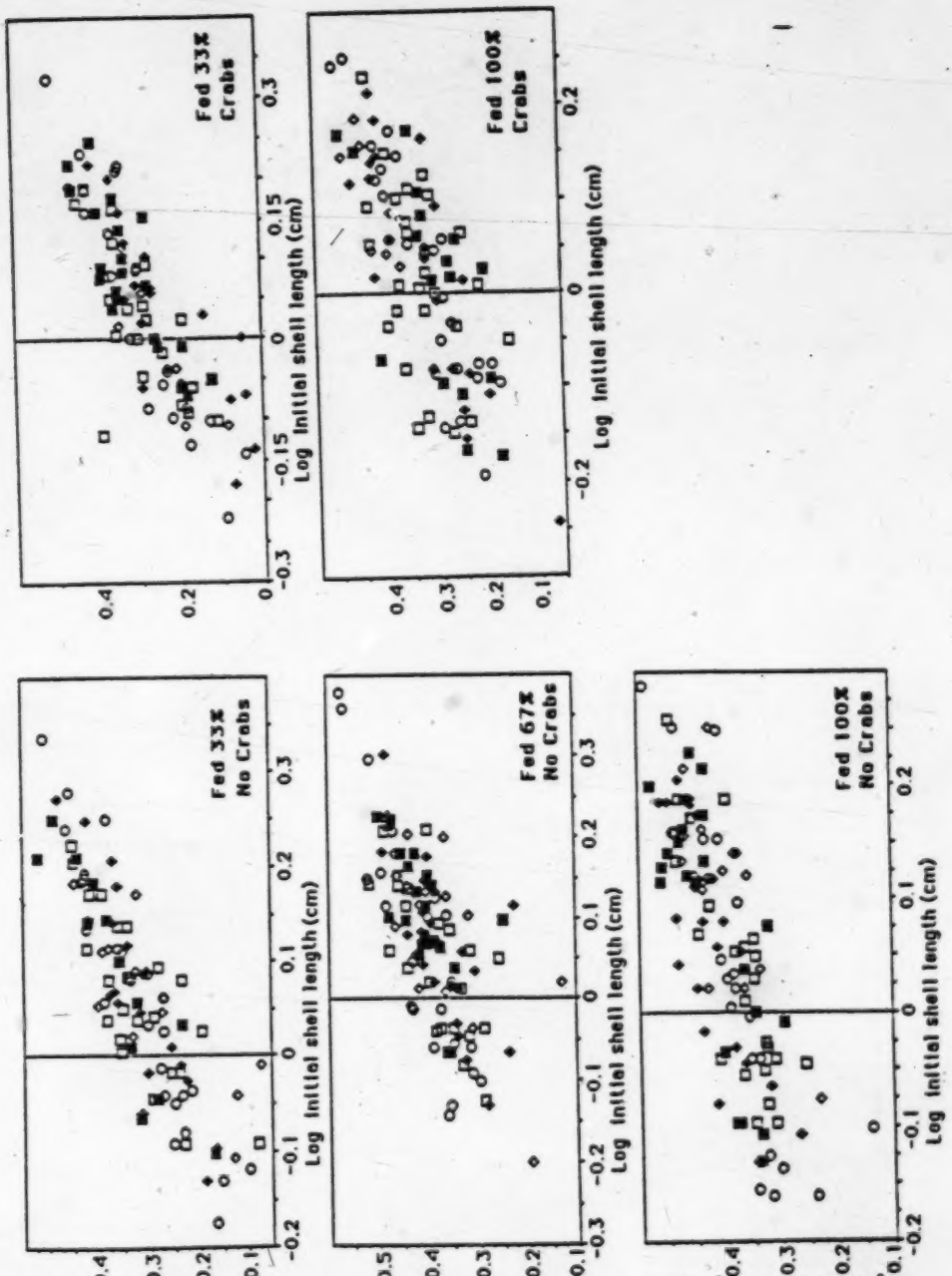
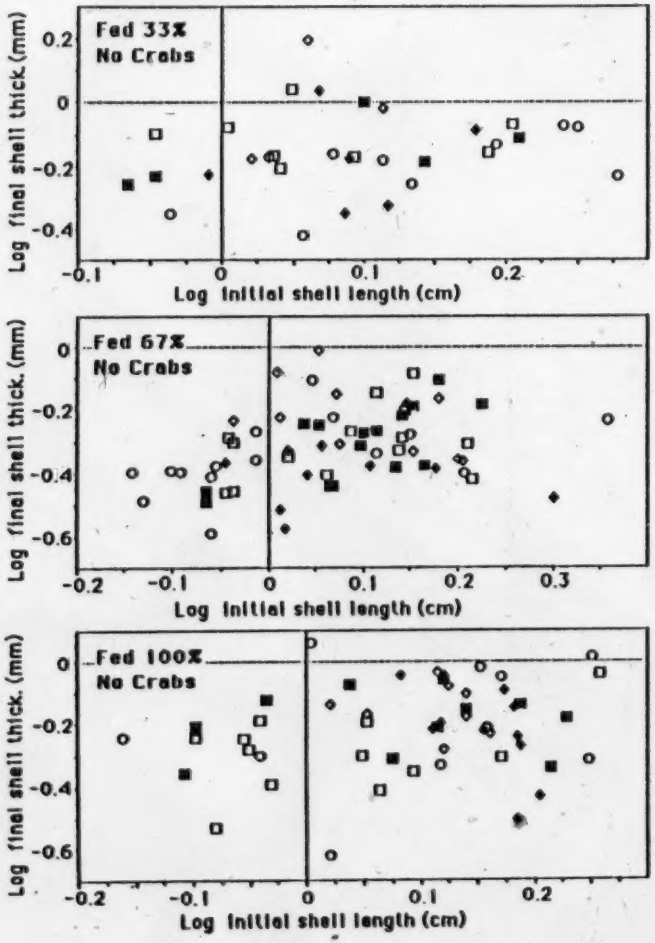

Fed 33% No Crabs
Fed 67% No Crabs
Fed 100% No Crabs
Fed 33% Crabs
Fed 100% Crabs
Log final shell length (cm)
Log initial shell length (cm)

Figure A4-16.

Scattergrams comparing variation among study sites with regard to log final shell thickness (mm) versus initial shell length (cm) at all food availabilities and crab exposures. ■ = Argyle Creek, ◇ = Aguilar Point, □ = Cattle Point ○ = Mar Vista, ◆ = Sanford Island.


Fed 33%
No Crabs
Log final shell thick. (mm)
Log initial shell length (cm)
Fed 67%
No Crabs
Log final shell thick. (mm)
Log initial shell length (cm)
Fed 100%
No Crabs
Log final shell thick. (mm)
Log initial shell length (cm)

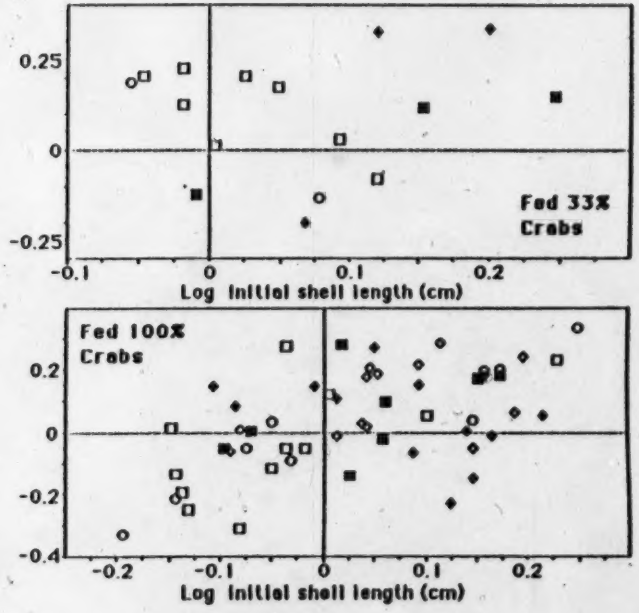

Fed 33%
Crabs
Log initial shell length (cm)
Fed 100%
Crabs
Log initial shell length (cm)

Figure A4-17.

Scattergrams comparing variation among study sites with regard to log translation rate (spiral growth/length change) versus spiral shell growth (cm) at all food availabilities and crab exposures. ■ = Argyle Creek, ◇ = Aguilar Point, □ = Cattle Point, ○ = Mar Vista, ◆ = Sanford Island.

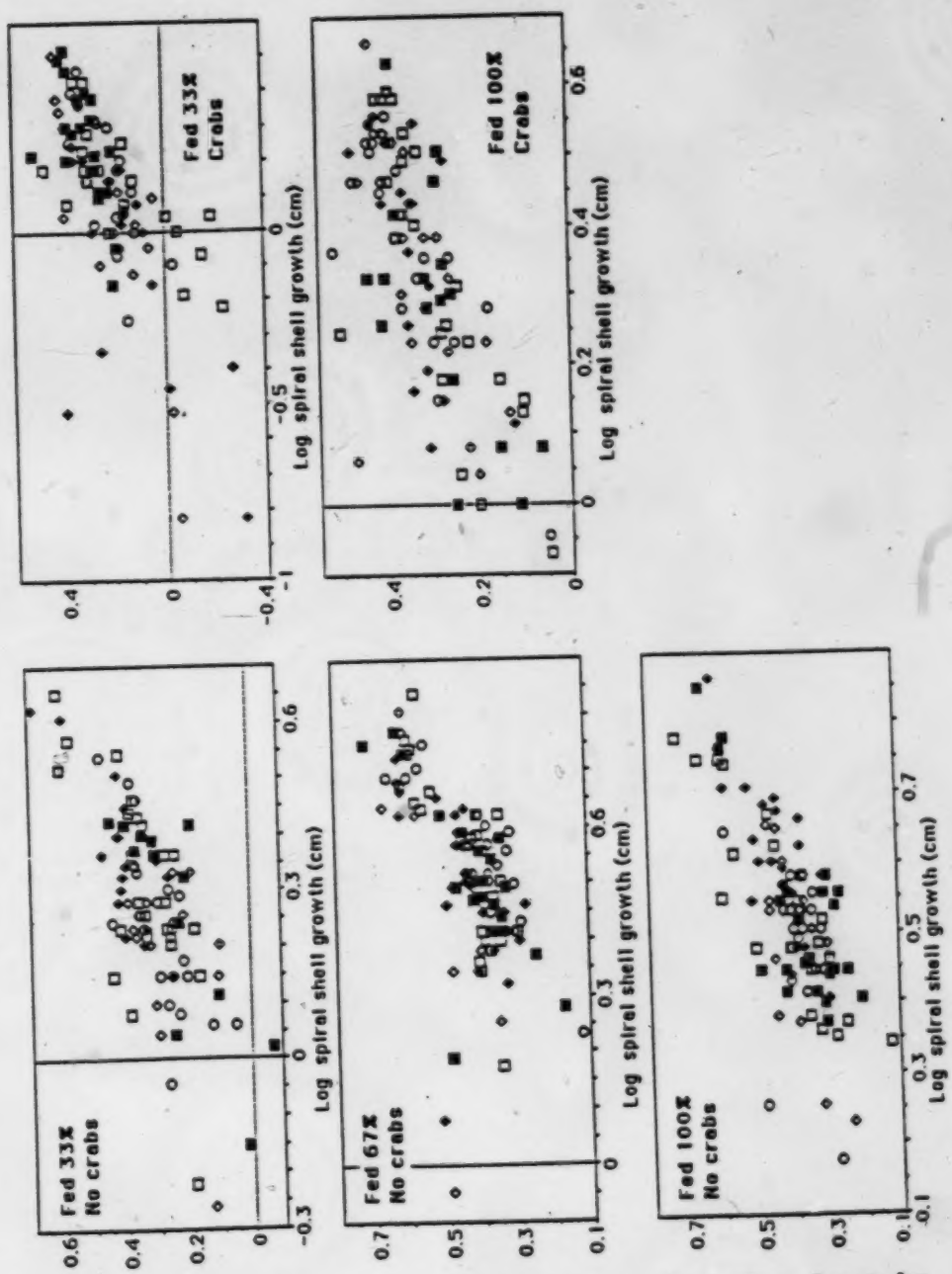

Fed 33% No crabs
Fed 67% No crabs
Fed 100% No crabs
Fed 33% Crabs
Fed 100% Crabs
Log spiral shell growth (cm)
Log spiral gr./length change

Figure A4-18.

Scattergrams comparing variation among study sites with regard to log final shell length (cm) versus log initial shell length (cm) at all water temperatures.

■ = Argyle Creek, □ = Mar Vista

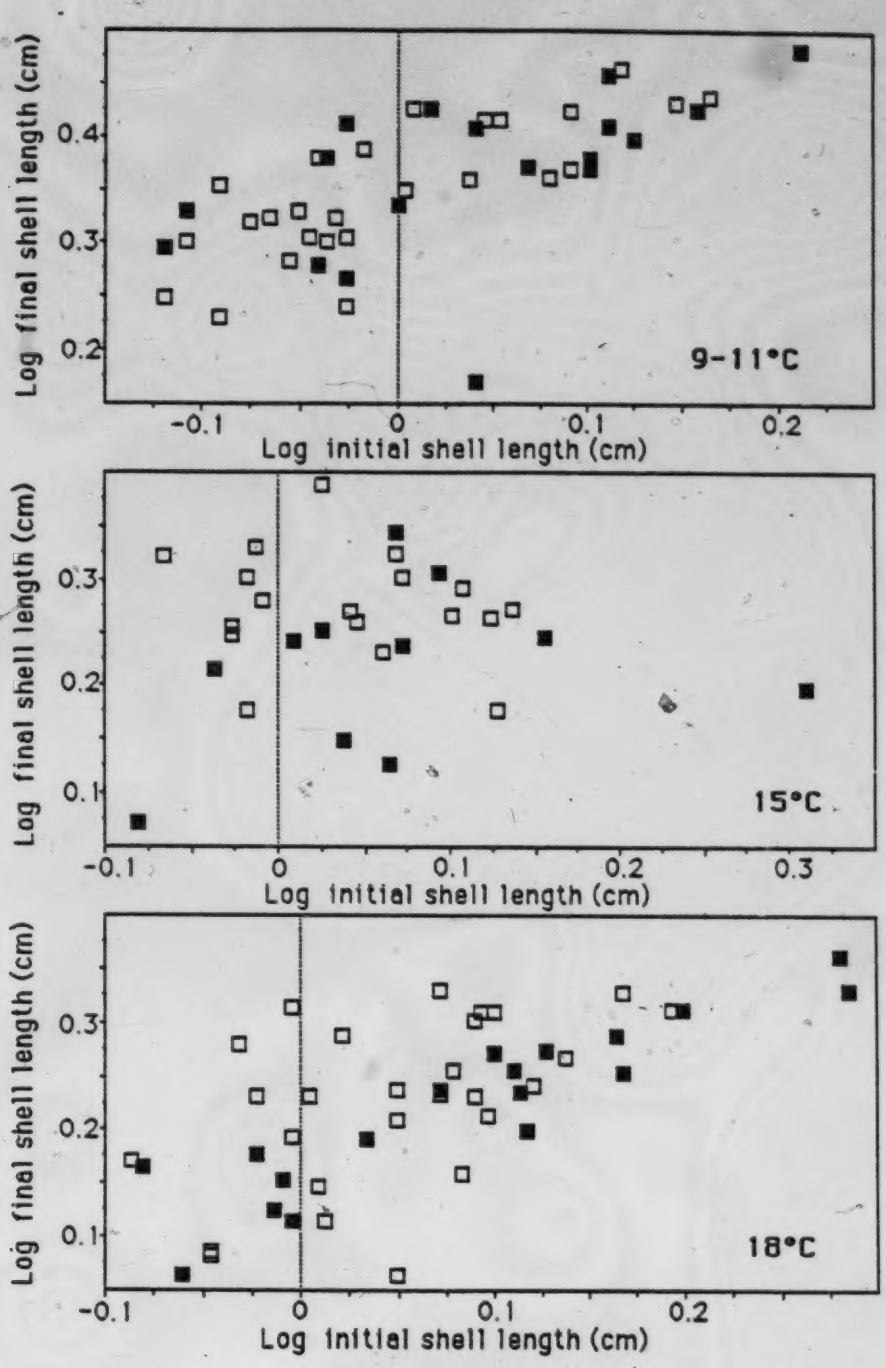

Log final shell length (cm)
0.4
0.3
0.2
9-11°C
-0.1
0
0.1
0.2
Log initial shell length (cm)
Log final shell length (cm)
0.3
0.2
0.1
15°C
-0.1
0
0.1
0.2
0.3
Log initial shell length (cm)
Log final shell length (cm)
0.3
0.2
0.1
18°C
-0.1
0
0.1
0.2
Log initial shell length (cm)

Figure A4-19.

Scattergrams comparing variation among study sites with regard to log final shell thickness (mm) versus log initial shell length (cm) at all water temperatures.

■ = Argyle Creek, □ = Mar Vista

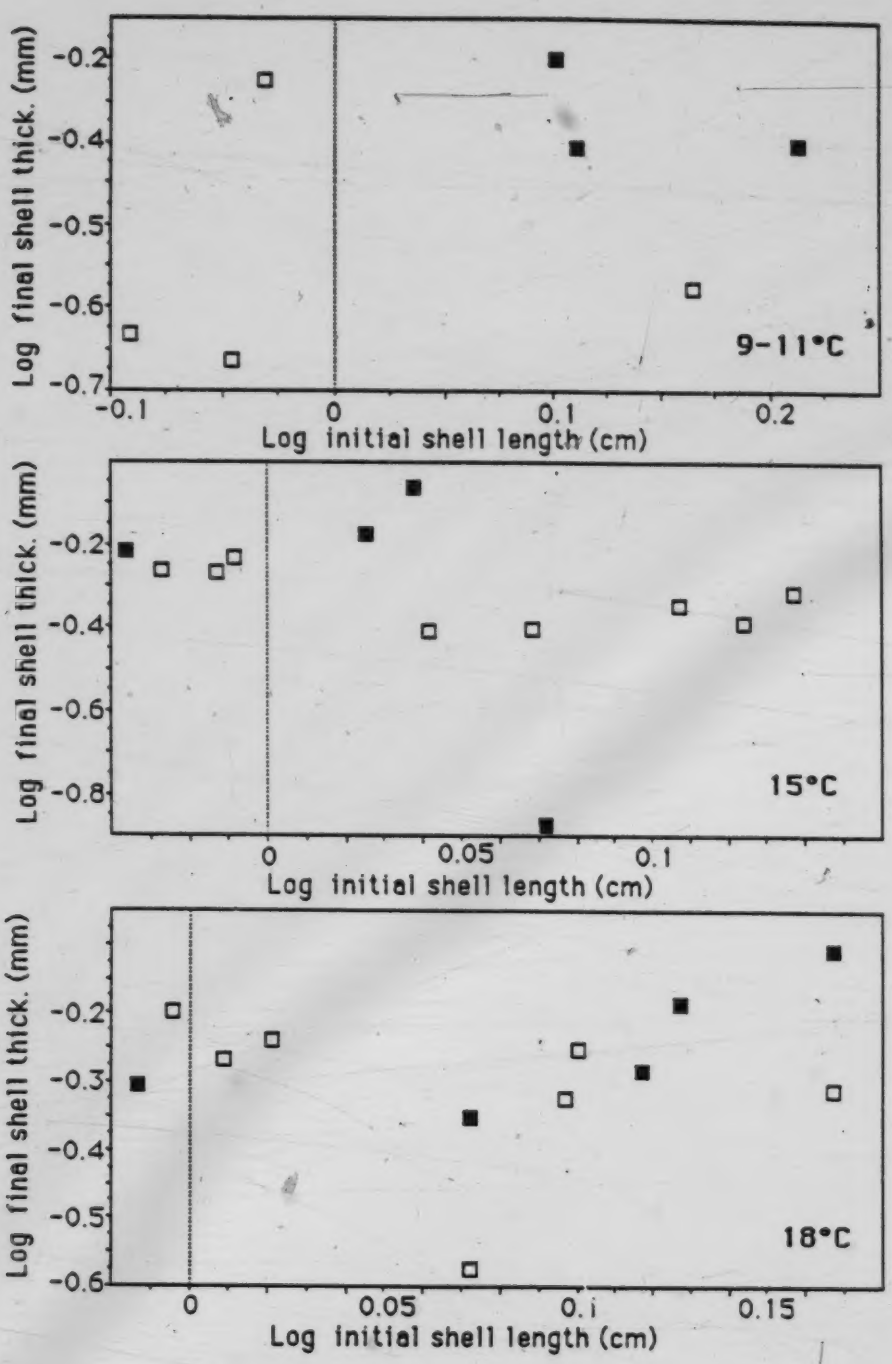
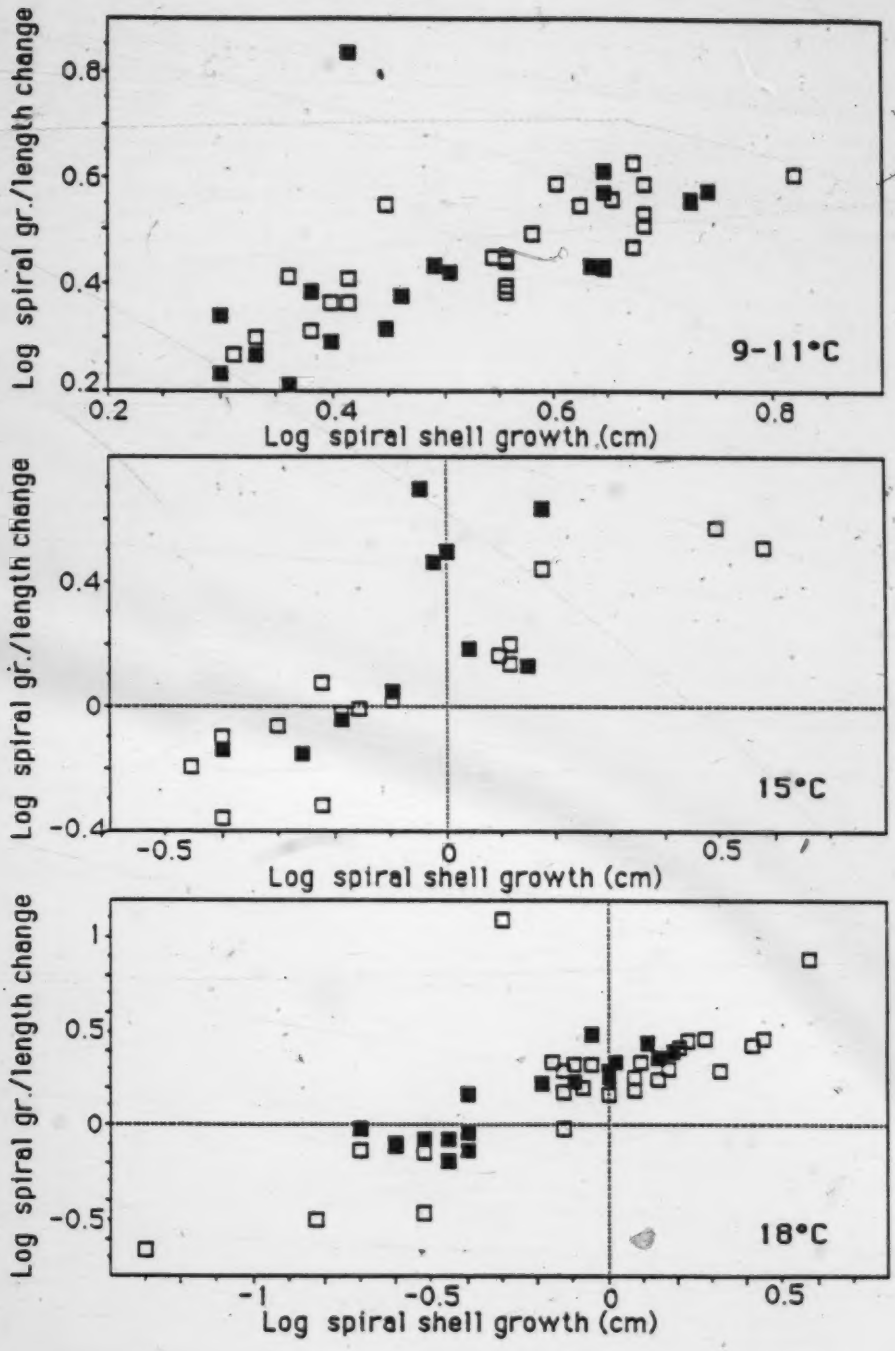

Log final shell thick. (mm)
-0.2
-0.4
-0.5
-0.6
-0.7
-0.1
0
0.1
0.2
Log initial shell length (cm)
9-11°C
Log final shell thick. (mm)
-0.2
-0.4
-0.6
-0.8
0
0.05
0.1
Log initial shell length (cm)
15°C
Log final shell thick. (mm)
-0.2
-0.3
-0.4
-0.5
-0.6
0
0.05
0.1
0.15
Log initial shell length (cm)
18°C

Figure A4-20.

Scattergrams comparing variation among study sites with regard to log translation rate (spiral growth/length change) versus spiral shell growth (cm) at all water temperatures. ■ = Argyle Creek, □ = Mar Vista


Log spiral gr./length change
0.8
0.6
0.4
0.2
0.2
0.4
0.6
0.8
Log spiral shell growth (cm)
9-11°C
Log spiral gr./length change
0.4
0
-0.4
-0.5
0
0.5
Log spiral shell growth (cm)
15°C
Log spiral gr./length change
1
0.5
0
-0.5
-1
-0.5
0
0.5
Log spiral shell growth (cm)
18°C

APPENDIX 5

Additional scattergrams from Chapter III.

Figure A5-1.

Scattergrams of the average thickness of the crossed lamellar layer (mm) versus final shell length (cm) for juvenile *Thais lamellose* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

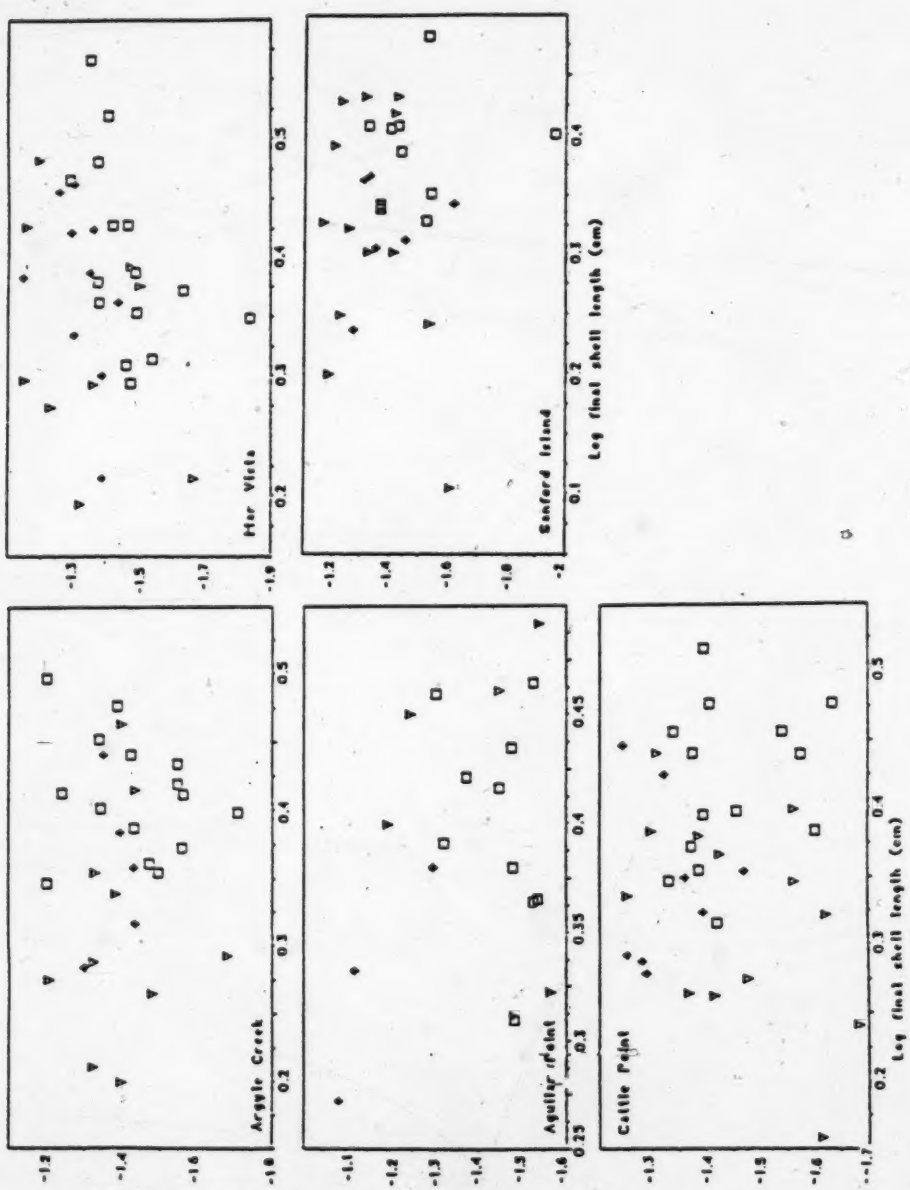

Log (average thickness of crossed lamellar structure) (mm)
Argyle Creek
Agulhir rfeint
Cattle Point
Mar Vista
Sanford Island
Log final shell length (cm)
Log final shell length (cm)

Figure A5-2.

Scattergrams of average thickness of the simple prismatic layer (mm) versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

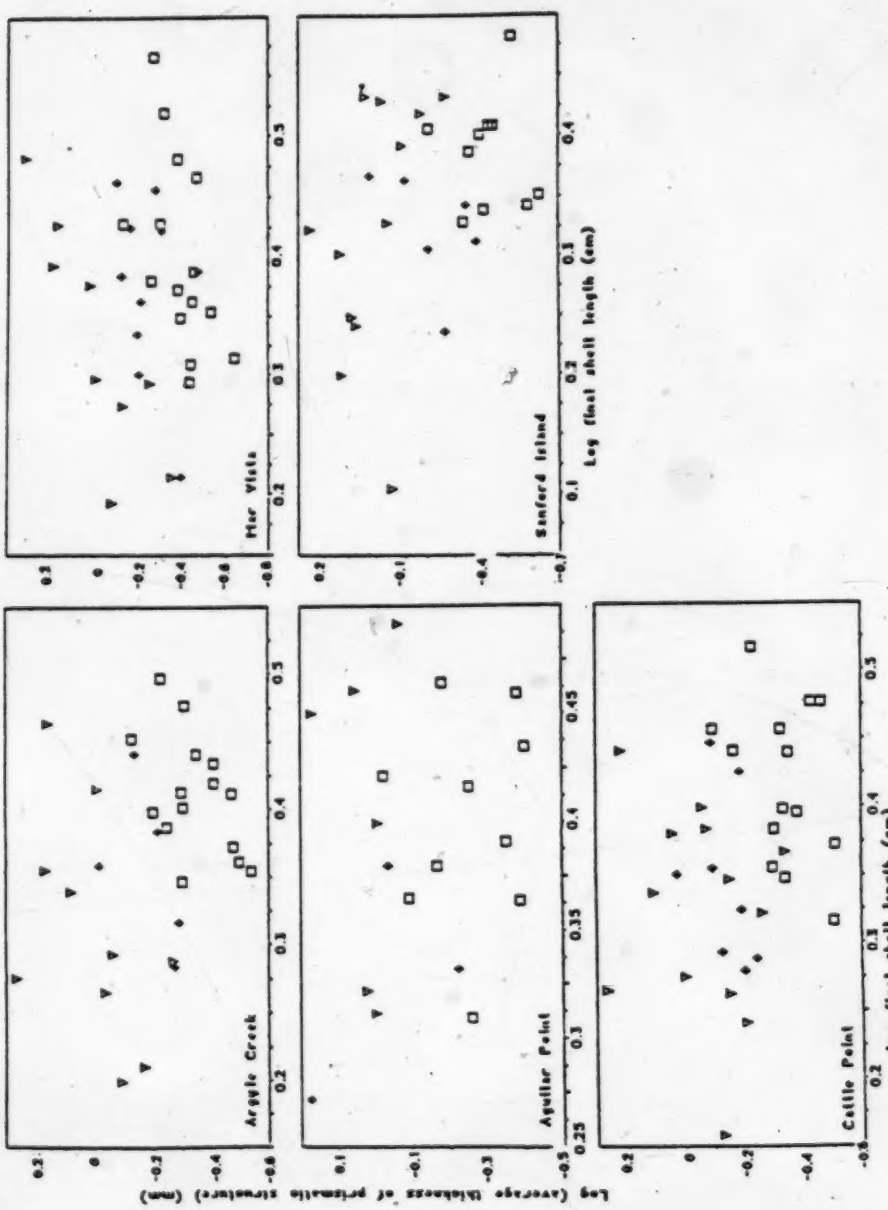

Log (average thickness of prismatic structure) (mm)
Argyle Creek
Aguilar Point
Cattle Point
Mar Vista
Sanford Island
Log final shell length (cm)
Log final shell length (cm)

Figure A5-3.

Scattergrams of the average thickness of the crossed lamellar layer over total shell thickness versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the absence of crabs, and at three food availabilities. ◆ = fed 33%, □ = fed 67%, ▽ = fed 100%.

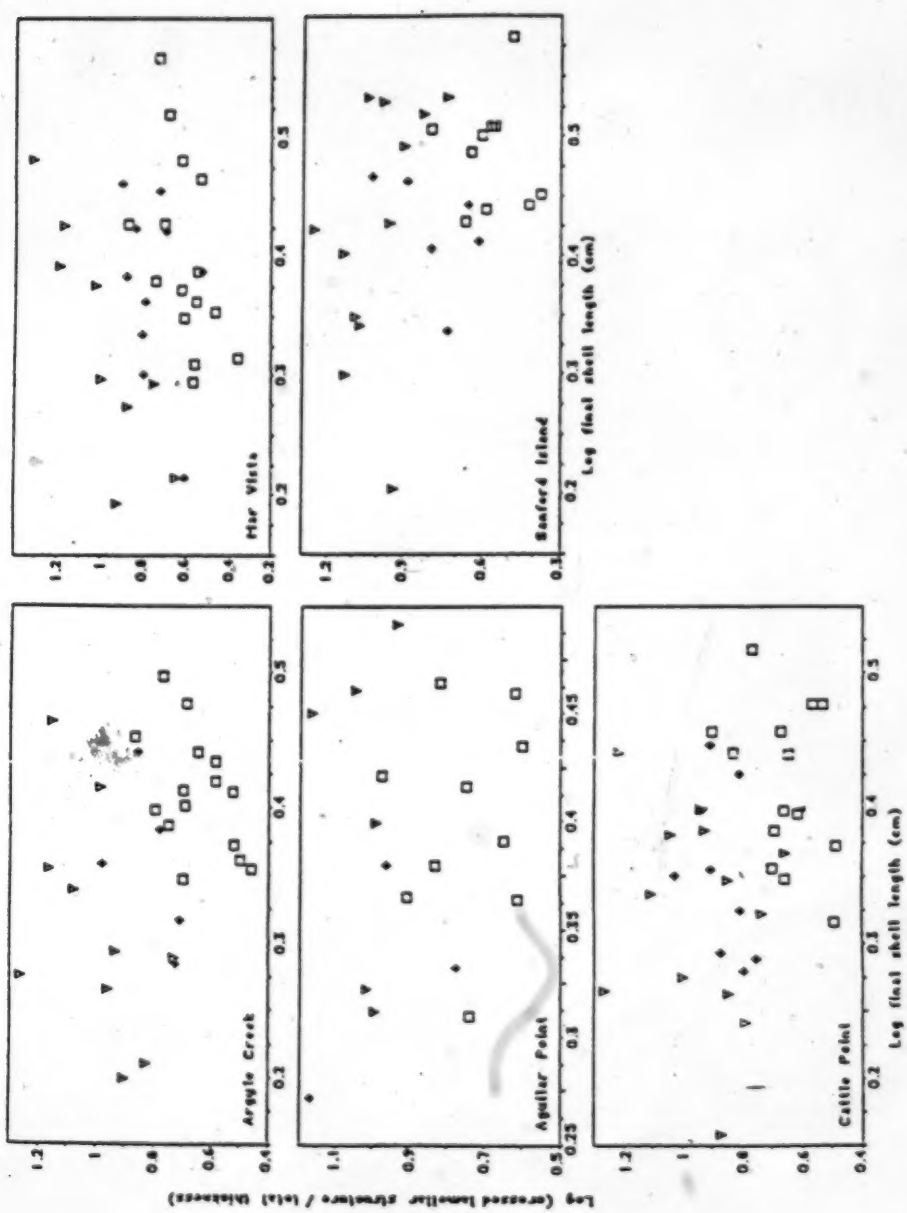

Log (crossed lamellar diameter / inlet diameter)
Argyle Creek
Agaller Point
Cattle Point
Mar Vista
Seaford Island
Log final shell length (cm)
Log final shell length (cm)

Figure A5-4.

Scattergrams of average thickness of crossed lamellar structure (mm) versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33&, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

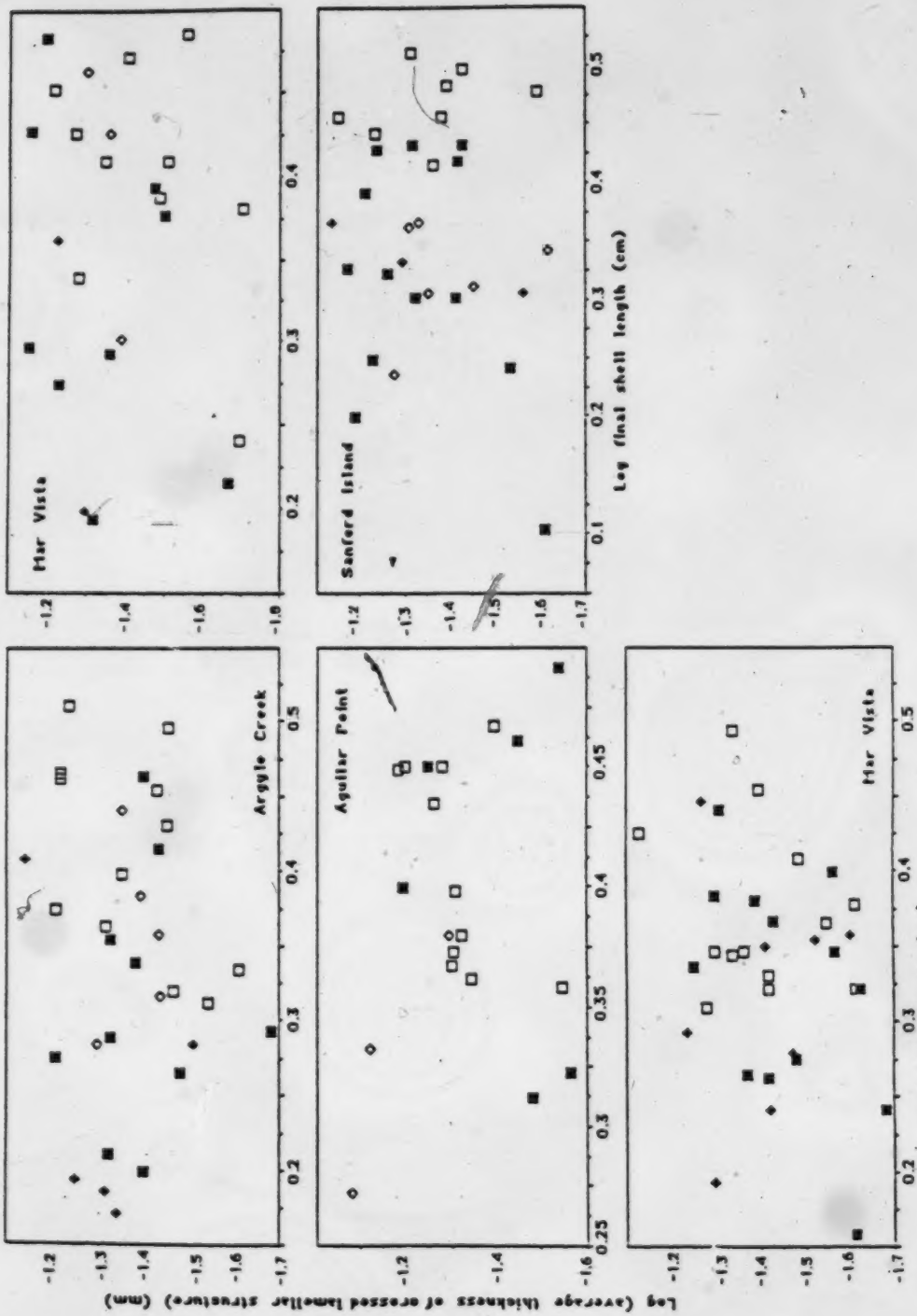

Argyle Creek
Aguilar Point
Mar Vista
Sanford Island
Mar Vista
Log (average thickness of crossed lamellar structure) (mm)
Log final shell length (cm)
Log final shell length (cm)

Figure A5-5.

Scattergrams of average thickness of simple prismatic structure (mm) versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

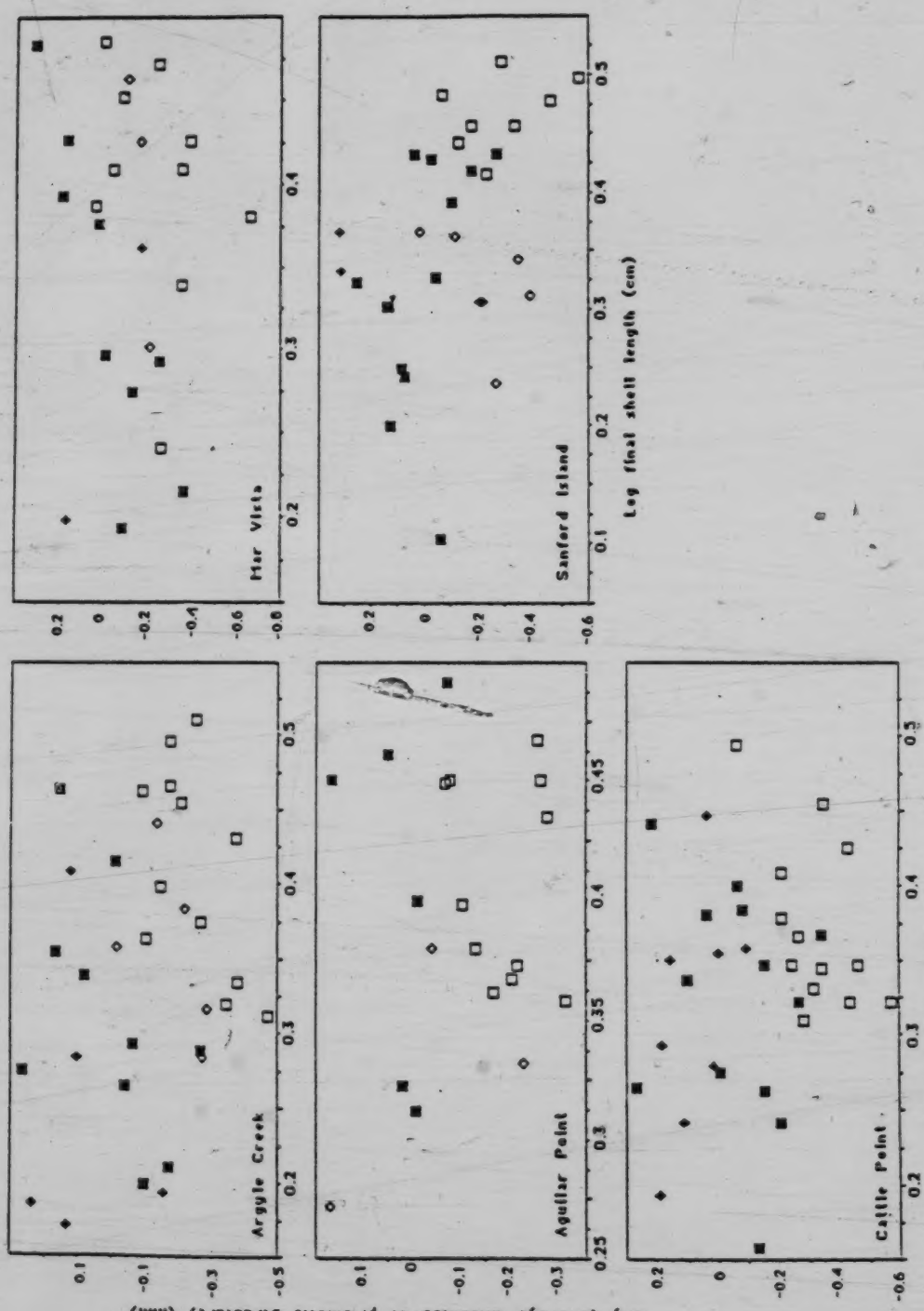

Log (average thickness of prismatic structure) (mm)
Argyle Creek
Aguilar Point
Cattle Point
Mar Vista
Sanford Island
Log final shell length (cm)
Log final shell length (cm)

Figure A5-6.

Scattergrams of the average thickness of crossed lamellar structure over total thickness versus final shell length (cm) for juvenile *Thais lamellosa* from five sites, raised in the laboratory at ambient water temperature, in the presence and absence of crabs, and at two food availabilities. ◇ = fed 33%, no crabs, ◆ = fed 33%, crabs, □ = fed 100%, no crabs, ■ = fed 100%, crabs.

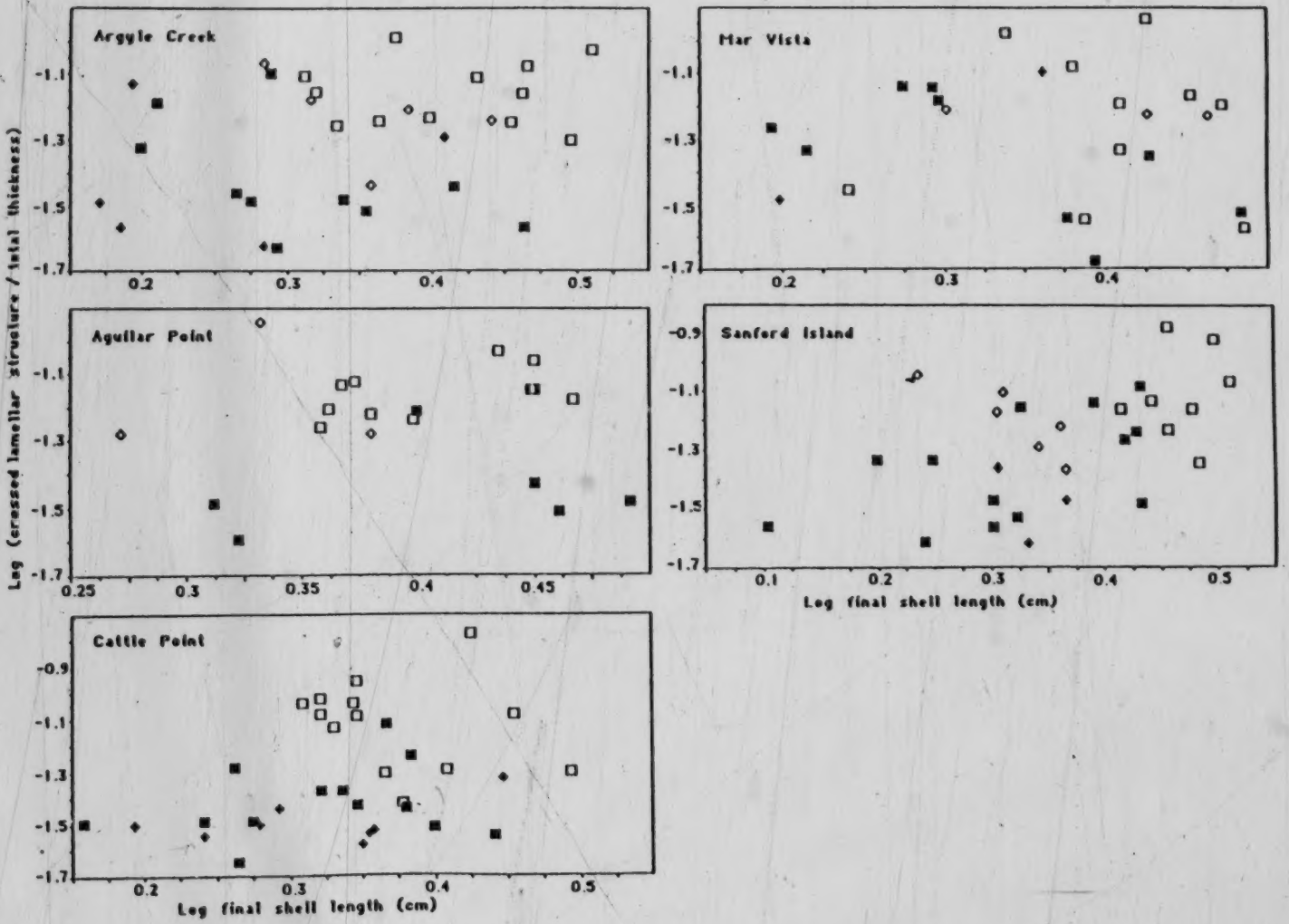

Argyle Creek
Mar Vista
Aguilar Point
Sanford Island
Cattle Point
Log (crossed lamellar structure / total thickness)
Log final shell length (cm)
Log final shell length (cm)

Figure A5-7.

A.

Scattergrams of average crossed lamellar thickness (mm) versus final shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures.

◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C

B.

Scattergrams of average simple prismatic layer thickness (mm) versus final shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures.

◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

C.

Scattergrams of average crossed lamellar thickness over total thickness versus final shell length (cm) for juvenile *Thais lamellosa* from two sites, raised in the laboratory in the absence of crabs, with 100% food, and at three water temperatures.

◆ = ambient water temperature (9-11°C), □ = 15°C, ▽ = 18°C.

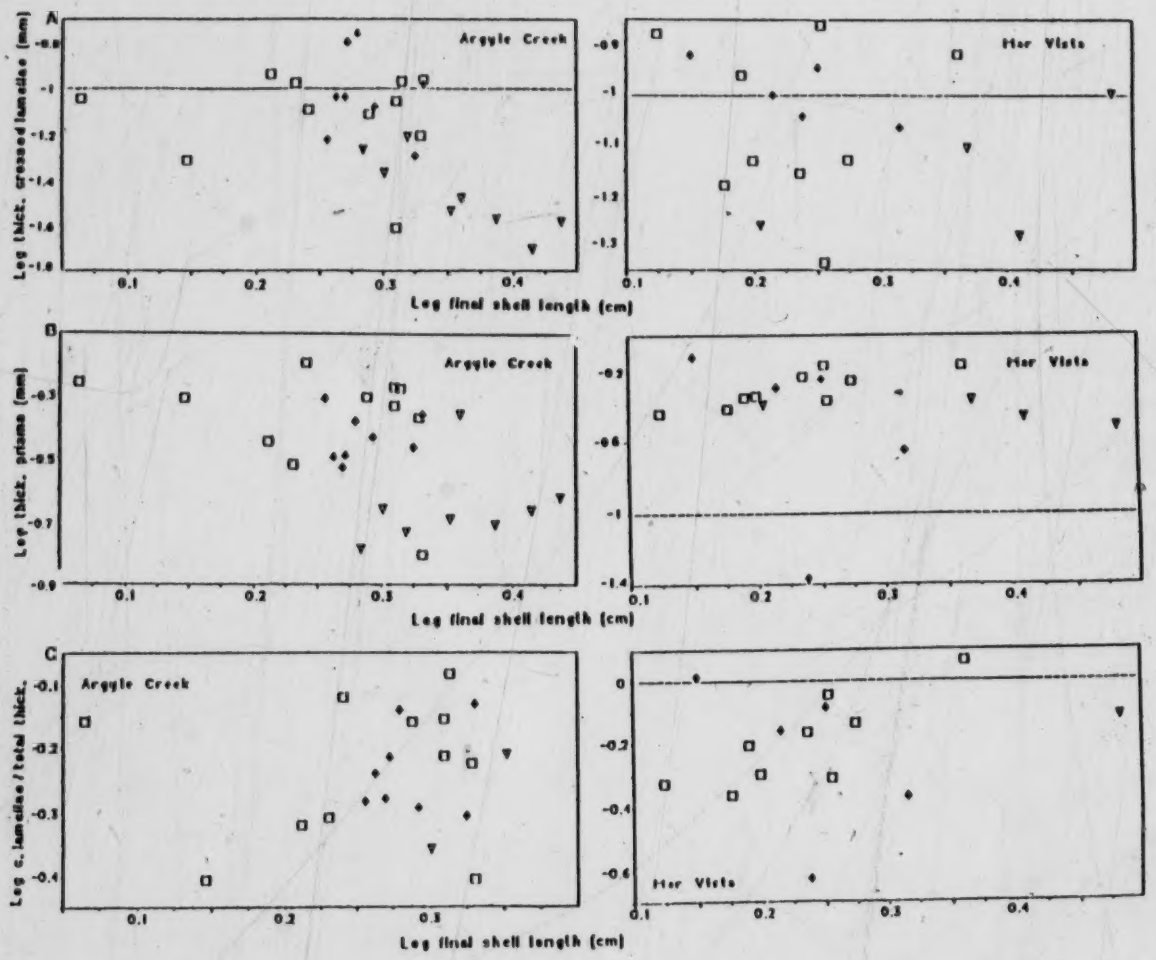

A
Argyle Creek
Log (thick. crossed lamellae (mm)
-0.9
-1
-1.2
-1.4
-1.6
-1.8
0.1
0.2
0.3
0.4
Log final shell length (cm)
Mar Vista
-0.9
-1
-1.1
-1.2
-1.3
B
Argyle Creek
Log (thick. prisms (mm)
-0.3
-0.5
-0.7
-0.9
Mar Vista
-0.4
-0.6
-1
-1.4
C
Argyle Creek
Log c. lamellae / total thick.
-0.1
-0.2
-0.3
-0.4
Mar Vista
0
-0.2
-0.4
-0.6

Figure A5-8.

Scattergrams comparing variation among study sites with regard to log crossed lamellar thickness/total shell thickness versus final shell length (cm) at all food availabilities and crab exposures. ■ = Argyle Creek, ◇ = Aguilar Point, □ = Cattle Point, ○ = Mar Vista, ◆ = Sanford Island.

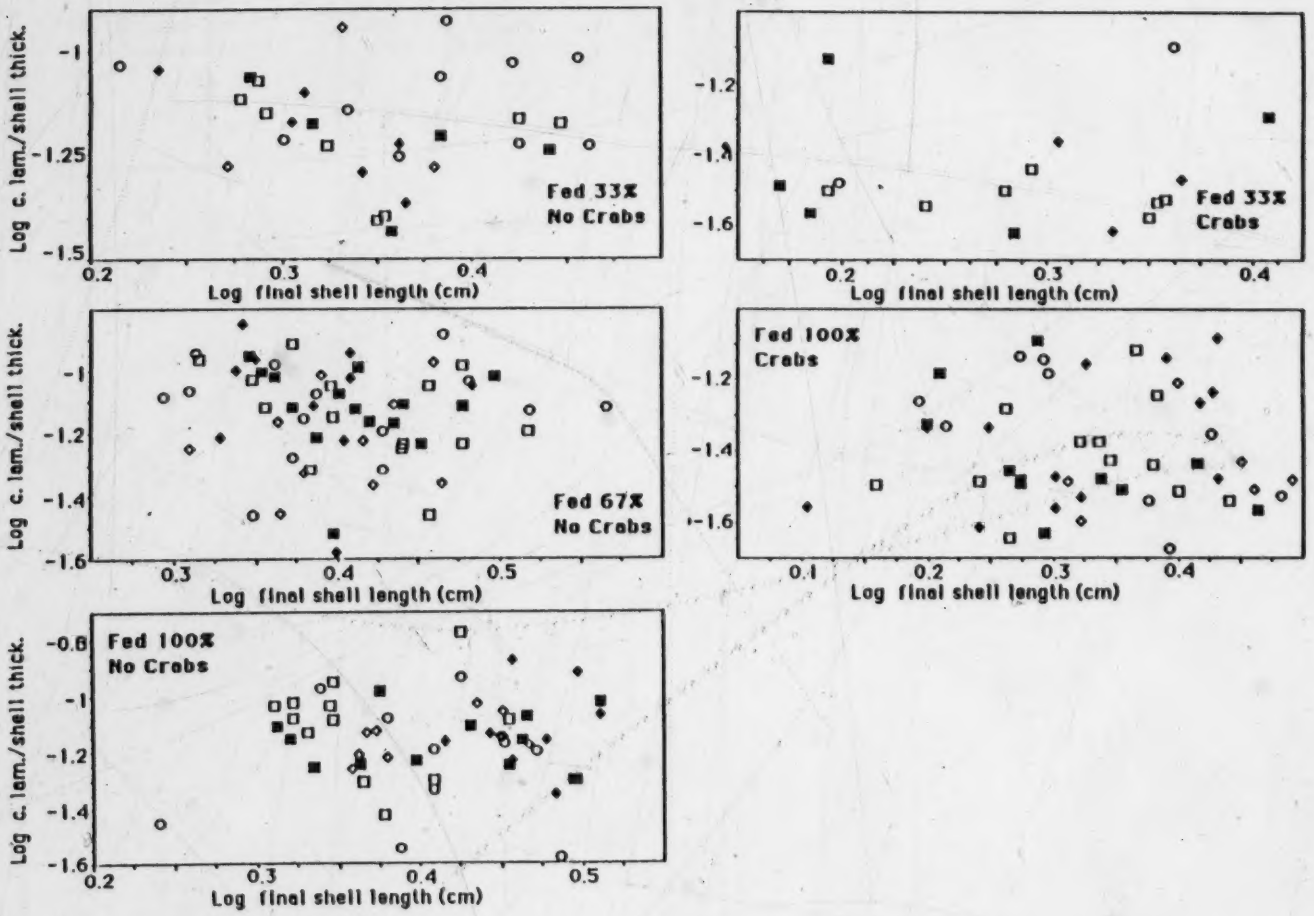
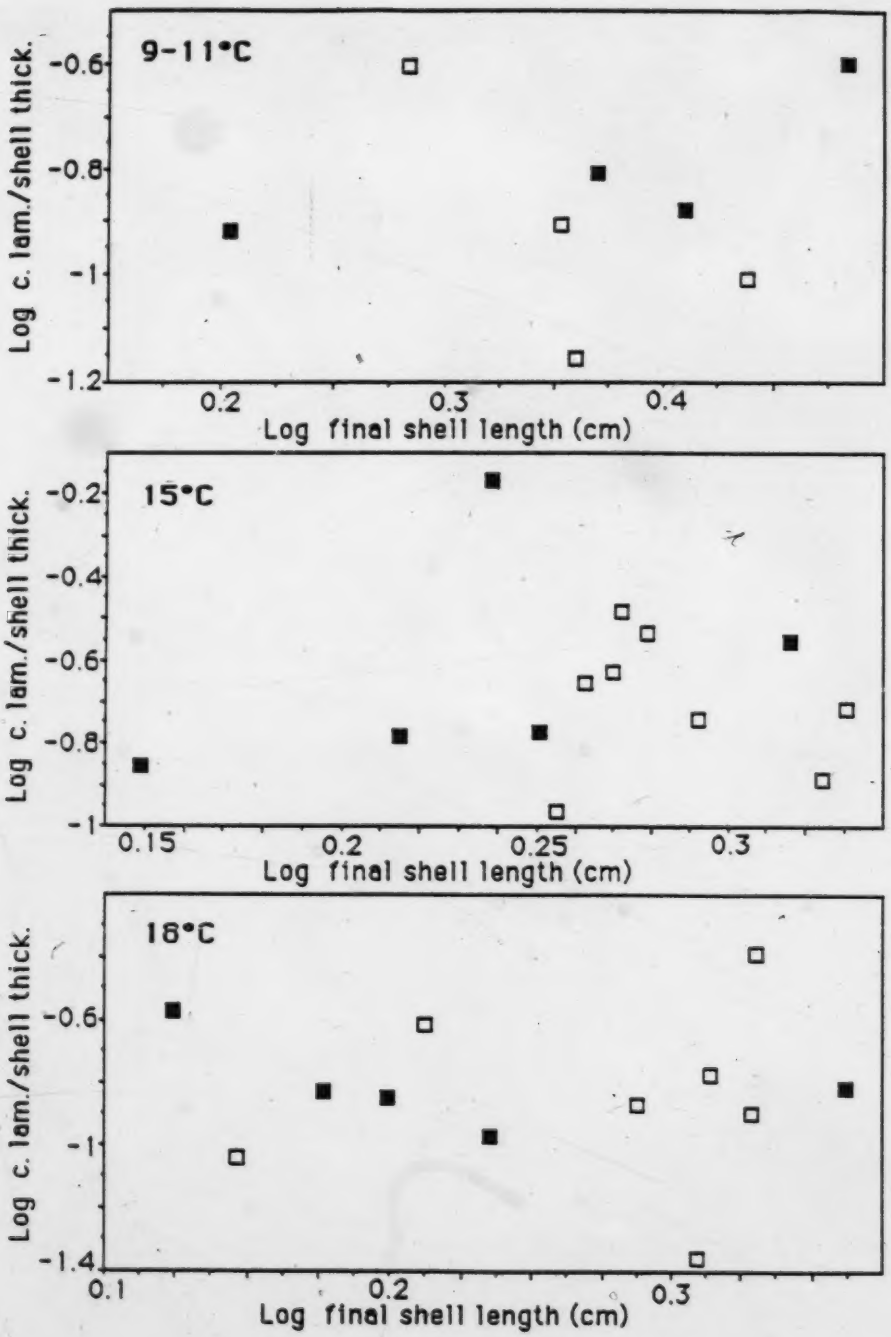

Log c. lam./shell thick.
Log final shell length (cm)
Fed 33%
No Crabs
Fed 33%
Crabs
Fed 67%
No Crabs
Fed 100%
Crabs
Fed 100%
No Crabs

Figure A5-9.

Scattergrams comparing variation among study sites with respect to log crossed lamellar thickness/total shell thickness versus final shell length (cm) at all water temperatures. ■ = Argyle Creek, □ = Mar Vista


9-11°C
Log c. lam./shell thick.
-0.6
-0.8
-1
-1.2
0.2
0.3
0.4
Log final shell length (cm)
15°C
Log c. lam./shell thick.
-0.2
-0.4
-0.6
-0.8
-1
0.15
0.2
0.25
0.3
Log final shell length (cm)
18°C
Log c. lam./shell thick.
-0.6
-1
-1.4
0.1
0.2
0.3
Log final shell length (cm)